Author:
Kelly, Richard

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Effects of environmental perturbation during the Late Triassic on the taxic diversity of British insects

Effects of environmental perturbation during the Late Triassic on the taxic diversity of British insects

Richard S. Kelly

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Abstract

The Late Triassic is a time of interest for investigating past periods of environmental perturbation as it experienced one of the most devasting extinction events in Earth history, the end Triassic extinction. Examining such past events is useful for understanding the broad patterns of ecosystem dynamics and how they respond to environmental change through time. Insects are incredibly diverse and integral to almost all terrestrial ecosystems. Therefore, understanding the dynamics of insect diversity and ecology through time provides insights into the processes that shape terrestrial ecosystems. A dataset of insect occurrence through the Triassic/Jurassic boundary (TJB) was compiled to analyse diversity dynamics and detect an extinction signal. Most insects from the Rhaetian/Hettangian were collected from the Severn Valley in Southwest England. From an initial assessment two main issues were found, namely, a lack of current discussion on the age of the insect-bearing deposits and the poor taxonomic state of the insects. Through stratigraphic revision, a series of insect-bearing horizons was established through the TJB. Then, the ~4000 British insect fossils were identified, dubious historical taxonomy was revised (nine species removed as *nomen dubia*), and newly discovered taxa were described (one new family, six new genera, and 16 new species). The compositions of the Rhaetian–Sinemurian assemblages were assessed in terms of species- and genus-level diversity and ecology. The results suggest that these assemblages are indeed distinct and do record a dramatic disruption to insect diversity in the Hettangian. However, the UK data are too patchy to establish long-term trends, so they were included in a dataset of all insects from the Late Triassic/Early Jurassic from the Palaeobiology Database. Through a series of analyses at a range of geographic, stratigraphic, and taxonomic levels compelling evidence was found for a dramatic decline in insect diversity at both local and global scales.

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Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

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Chapter 1. General introduction

The Triassic/Jurassic boundary (TJB) is of interest for investigating past periods of environmental perturbation and climate change and how such perturbations affect biodiversity. Examining past events is useful for understanding broader patterns in ecosystem dynamics and extinctions through time. Climate is constantly changing, if a species cannot adapt to those changes or cannot compete with more adaptable neighbours, then the species may go extinct. Usually, change is at a rate to which most species can adapt, meaning that the rate of extinction is not high enough to cause a catastrophic ecosystem breakdown, rather there is a regular process of species turnover which is considered a background extinction rate.

Turnover of species is an ongoing process but there are periods where species turnover is particularly high, and higher levels of extinction are often coupled with higher levels of origination of new species. This is usually due to a greater rate of change in certain external forces than usual, e.g. rise in atmospheric temperature, making the environment more hostile because it is changing too quickly for many species to adapt and therefore there is a higher probability of species going extinct. In these situations, the system is perturbed and there may be a high loss of taxa, but functional diversity and therefore ecosystem stability may not necessarily be compromised.

Then there are catastrophic break-downs of ecosystems in response to extreme environmental perturbation, often caused by large-scale events such as massive volcanic activity or bolide impact. During such an event the climate is perturbed to a point where the environment changes at a rate to which most taxa cannot adapt. In such a situation, species go extinct at a far greater rate than they are being replaced, leading to loss of key functional elements, breakdown of food webs, and potentially large-scale ecosystem collapse. This describes a mass extinction, which is usually a specific event or chain of events leading to ecosystem collapse and an impoverished biosphere until new ecosystems evolve. If an event is large enough to have a catastrophic effect on Earth's climate then ecosystem collapse may be global in scale affecting the whole biosphere.

1.1 Triassic/Jurassic boundary and Late Triassic mass extinctions

Towards the end of the Triassic and the transition to the Early Jurassic there is evidence for a global scale mass extinction event (end Triassic extinction, ETE; or recently Late Triassic extinction, LTE). This was one of five of the most destructive events known from Earth's history and is considered to have been triggered by the eruption of the Central Atlantic Magmatic Province (CAMP) (Hesselbo et al., 2002; Bond and Wignall, 2014). Most recent studies consider warming caused by an increase in volcanogenic CO_2 as the main kill mechanism (Preto et al., 2010), possibly exacerbated by a positive feedback loop from the effects of warming on seafloor methane hydrates (Pálfy et al., 2001). Carbon

isotope excursions (CIEs) have been recorded from Nevada (Guex et al., 2004), Austria (Hillebrandt et al., 2013), the UK (Hesselbo et al., 2002), Hungary (Korte and Kozur, 2011), and Canada (Williford et al., 2007). These deposits record a series of negative $\delta^{13}C$ excursions leading to the TJB (Fig. 1.1), which have been inferred to be caused by CAMP volcanism. At several of the sites a small positive $\delta^{13}C$ excursion has been observed after the initial CIE, and then a 'main' negative CIE which was longer in duration with its onset slightly preceding the first occurrence of Jurassic ammonites (Ruhl et al., 2009).

The stratigraphy of the Late Triassic is problematic and establishing the timing of events can be difficult as there is little consensus on stage boundary ages, magnetostratigraphic or cyclostratigraphic timelines, or correlations between global successions with Gradstein et al. (2012) considering the Late Triassic to comprise a "glaring lack of age dates, tenuous correlations and competing but startlingly different stage models". Recent studies have attempted to establish a timeline of events across the TJB by correlating sections from different countries and with each new study comes fresh insights and the Late Triassic timeline can change dramatically. Historically, in British stratigraphy, the base of the Jurassic system was placed at the base of the Planorbis Zone (Hounslow et al., 2004) with the mostly non-ammonite bearing pre-planorbis beds preceding it. The Global Stratotype Section and Point (GSSP) for the base of the Jurassic System (base of the Hettangian) was chosen in a section from Kuhjoch Pass, Tyrol, Austria (Hillebrandt et al., 2007, 2013), with the Tilmani Zone as the lowest ammonite zone recognised. The characteristic ammonites *Psiloceras tilmani* and *P. spelae* of the lowermost Jurassic are not found in British deposits, the first occurrence of Jurassic ammonites is with *P. erugatum* in the upper pre-planorbis beds (Donovan, 1966; Page and Bloos, 1995). Therefore, British sections have been correlated with European ones mostly based on the carbon isotope and palynological records of St Audrie's Bay, Somerset, a key reference section for this time interval. An initial CIE in the Cotham Member of the Lilstock Formation and the main CIE, coinciding with a period of black shale deposition, in the lower Blue Lias Formation (Hesselbo et al., 2002). The prevailing view for the past few years has been that the initial CIE at the St Audrie's Bay section was contemporaneous with the sharp negative CIE at Kuhjoch, which corresponded with the last occurrence of the ammonite *Choristoceras marshi*, marking the end of the Marshi Zone and the onset of the ETE (Ruhl et al., 2009, 2010; Hillebrandt et al., 2013). This inferred that the main extinction event occurred in the uppermost Triassic and that the base of the Jurassic system was at or close to the base of the Blue Lias Formation, including the pre-planorbis beds (Page, 2010; Cope, 2012). Additionally, two main pulses of CAMP volcanism have been correlated between terrestrial and marine sections with the first unit of CAMP basalts from Morocco correlating with the onset of the initial CIE of St Audrie's Bay, with a more prolonged pulse in the uppermost Triassic (Deenen et al., 2010).

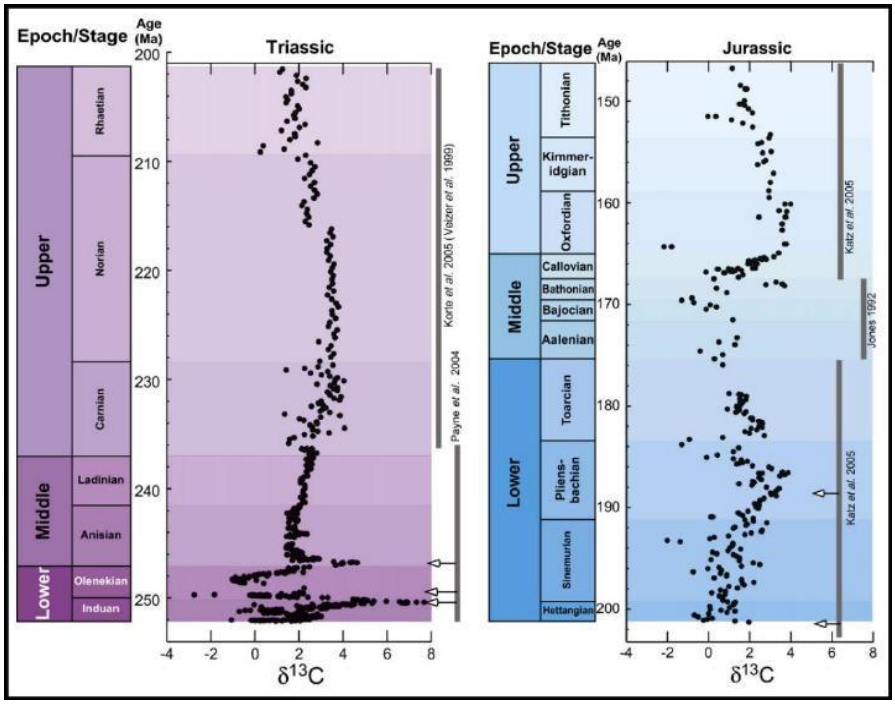

Figure 1.1. The Triassic and Jurassic timescales and carbon isotope record (Gradstein et al., 2012). Arrows indicate well-studied excursions which indicate changing temperatures.

As further research is carried out and the timeline is refined so too is the series of events leading to the TJB. Lindström et al. (2017) offered an alternative scenario based on correlations of biologic (ammonites and pollen), geochemical (CIEs), and radiometric (U/Pb) constraints. Briefly, they discussed the occurrence of perturbed ecosystems prior to the initial CIE for marine fauna (Mander et al., 2008; Clémence et al., 2010) and terrestrial vegetation (van de Schootbrugge et al., 2009). They considered the fern pollen *Polypodiisporites polymicroforatus* to have a temporally restricted distribution that can be correlated accurately throughout northwest Europe and that the upper boundary of the Marshi Zone should correspond to the lower boundary of the period of time in which this pollen was the most abundant, and thus, the main extinction event. In the UK, this pushed the ETE back to an older, more prolonged CIE in the middle of the Westbury Formation that they referred to as the "Marshi CIE". This CIE was accompanied by a major marine transgression in northwest Europe, with a period of regression during the extinction period culminating in another major transgression following the TJB.

In the UK, the dark, organic-rich shales of the Westbury Formation are found in deposits prior those that record the main extinctions of marine invertebrates as considered by Wignall and Bond (2008) and Mander et al. (2008). Lindström et al. (2017) also considered that the CAMP basalt pulses occurred alongside or prior to the Marshi CIE, citing discrepancies in the different reports of U/Pb ages for these beds. Panfili et al. (2019) offered a correlation of the CAMP basalts from Morocco with Kuhjoch and St Audrie's Bay and discussed both possible scenarios, that the lower CAMP basalt unit

corresponds to the initial CIE of Hesselbo et al. (2002) or with the Marshi CIE of Lindström et al. (2017). Other recent studies have argued against the validity of palynological correlations, e.g. Zaffani et al. (2018) correlated a section from the Lombardy Basin in Italy and considered the initial CIE of St Audrie's Bay to correspond with a similar negative CIE in their section and discuss its connection with CAMP basalts and the onset of the ETE. They refer to the Marshi CIE of Lindström et al. (2017) as the precursor CIE. The timeline of events in the Late Triassic is still very much subject to discussion and new studies can bring massive changes to our interpretations of the geological record at this time. The new chronology of Lindström et al. places the ETE in the Westbury Formation, much earlier than the Lilstock Formation: Cotham Member, where it was traditionally considered. This has ramifications for the analysis in the project and will be discussed further in later chapters.

The validity of the ETE is widely accepted (Raup and Sepkoski, 1982; Benton, 1995; Stanley, 2016), but it has been queried by, e.g. Lucas and Tanner (2018), who argued that global data sets may suffer from a compiled correlation effect and that stage level analyses are too low resolution resulting in extinctions becoming clumped at stage boundaries whereas they are more realistically spread throughout the stage with much more complex dynamics. Whereas, artificially spreading out the extinction dates achieves the gradual decline effect Lucas and Tanner prefer. The answer is to improve the time scale and use smaller time bins. Geographic scale is also an important factor to consider. Lucas et al. (2011) considered the record of floral turnover during the TJB interval to indicate separate regional perturbations and not a global extinction event. Lucas and Tanner (2007) suggested that some floral turnovers predated CAMP, especially in the Newark Basin. However, this is debated, and some were found to be contemporaneous with CAMP presumably being caused by it (van de Schootbrugge et al., 2009). It has been argued that any uncertainty is more due to the lack of large-scale studies of macroplants. Arguably, the best macroplant record across the TJB is from Greenland (McElwain et al., 2009) which records >80% loss of species and ~17% loss of genera across the boundary. This is indeed an extreme decline in macroplant diversity, but it is difficult to ascertain whether this is indicative of a global signal without other macroplant records from precisely correlated global sections.

1.2 Insects and extinctions

Insects are one of the most diverse group of animals today (Fig. 1.2) and are important parts of almost all terrestrial and freshwater habitats, and some marine habitats, and have been for most of their history (Grimaldi and Engel, 2005). There is much research carried out into the spatial variation of extant insects, but relatively little on variation through deep time. To understand how perturbations to the environment can affect insects it is important to build up accurate accounts of entomofaunas both spatially and temporally and to understand how large-scale events, such as mass extinctions, affected them in the past.

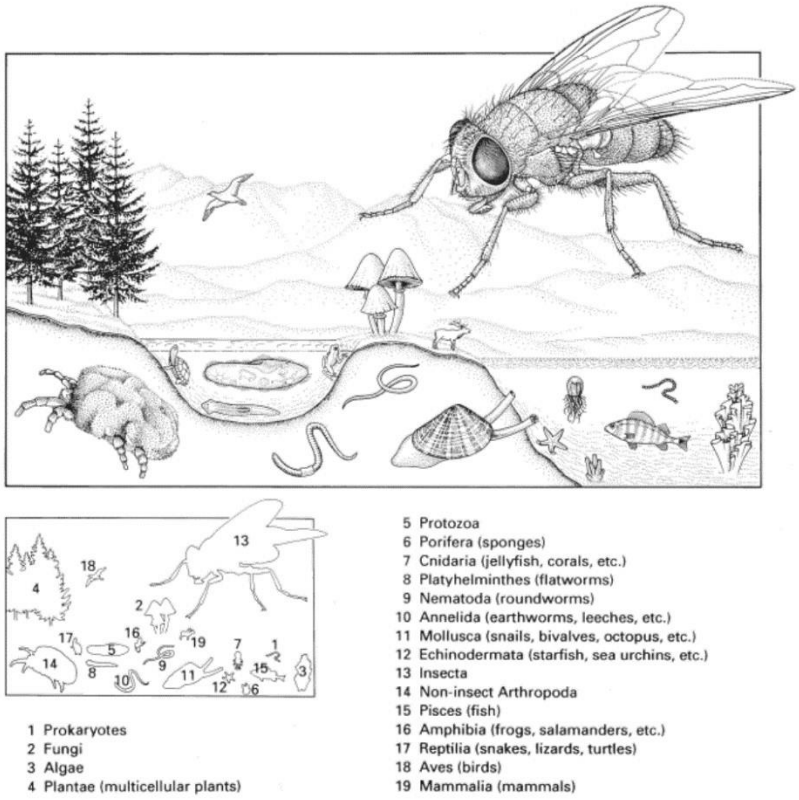

Figure 1.2. A specioscape illustrating the relative diversity of life in terms of species described, the larger the animal the more described species (Gullan and Cranston, 2010).

1.2.1 Brief history of British palaeoentomological research

Although fossilised organisms have been studied and written about since Ancient Greece and Persia the more modern systematic study of palaeontology emerged sometime in the 17th century. Palaeoentomology was rather late to the game, with the first real interest in collecting and describing fossil insects emerging in late 18th century Germany (Bloch, 1776). The early to middle 19th century saw a great deal of fossil insect collecting in England with Rev. Peter Brodie's seminal synoptic study on British Mesozoic insects (Brodie, 1845). Brodie describes the large collection of insects he amassed including the Triassic/Jurassic collection used in this project. This monograph remains one of the primary sources of literature for British Mesozoic insects. Brodie also published an array of papers regarding fossil insects throughout the mid to late 19th century before his death in 1898. Many of these papers were notes on various areas of stratigraphic interest (Brodie, 1843, 1847, 1850, 1853, 1854, 1857a, 1857b, 1865, 1866; Brodie and Buckman, 1845) or individual specimens/taxa of interest (e.g. Brodie, 1849). Many of the specimens collected by Brodie were subsequently named by Giebel (1856) and many were later revised/described by Anton Handlirsch (Handlirsch, 1906, 1939) based primarily on the figures provided by Westwood in Brodie (1845) (see Fig. 1.3 for examples). A summary of the fossil insects known from the Mesozoic of Britain and other countries was published by Goss (1879) with a list of all known species at the time.

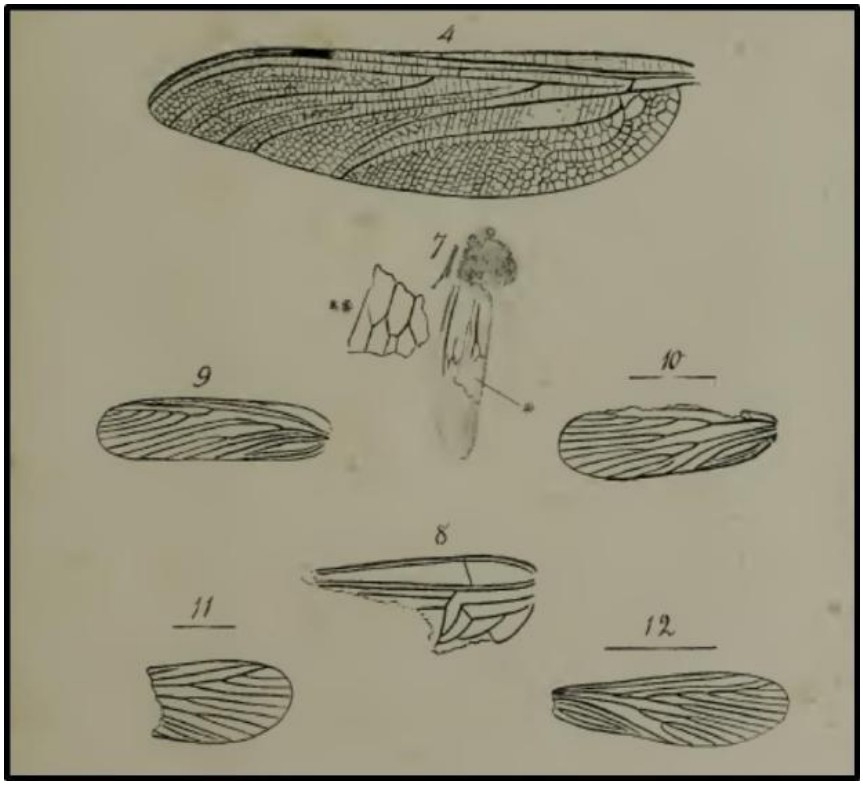

Figure 1.3. Examples of historical insect holotype figures from Brodie (1845).

Not all the Brodie collection remained in the UK. From reading personal correspondence written by Brodie to several museums it was clear that he was an avid fossil trader and was keen to trade parts of his fossil insect collection with other collectors. The Ralph Dupuy Lacoe collection held at the National Museum of Natural History, Smithsonian Institute in the United States includes 39 specimens collected by Brodie. These specimens were examined by Theodore Dru Alison Cockerell and several new taxa were described (Cockerell, 1915), some of which were further revised by Handlirsch (1939). The Harvard Museum of Comparative Zoology also holds a small collection of Brodie's insects which Brodie sent Samuel Scudder at the then Boston Society of Natural History, which became the Boston Museum of Science. The fossil collection ended up at Harvard University, but a sizable collection of letters written between 1865 and 1897 to Scudder from Brodie is still held at the Museum of Science. Along with other collections of letters held at the Natural History Museum, London and Oxford University Museum of Natural History they provide interesting details of Victorian fossil collecting.

During the early 20th century the British entomologist Robin John Tillyard, and German palaeontologist, Frederick Everard Zeuner, took an interest in British fossil insects. Tillyard emigrated to Australia in 1904 (Imms, 1938) and is probably better known for his work on Australian insects. Zeuner was known for his work on Quaternary stratigraphy in Germany but moved to England in 1934 to escape Nazi persecution and returned to work on fossil insects at the then British Museum (Natural History) (Fairbridge, 1999). Tillyard focussed mainly on dragonflies and damselflies (Odonata) publishing one of the key early texts on odonate biology (Tillyard, 1917). Concerning British

Triassic/Jurassic insects Tillyard published two key texts describing many of the odonates in the Brodie collection (Tillyard, 1925) and many of the "panorpoid" insects of the orders Lepidoptera (moths and butterflies), Neuroptera (lacewings), Mecoptera (scorpionflies), Trichoptera (caddisflies), and Diptera (true flies) (Tillyard, 1933). These are important contributions to our understanding of these insects and although they do cover a considerable amount of Triassic/Jurassic taxa many of the descriptions do not stand up to scrutiny based on current understanding of insect taxonomy.

Zeuner mostly published works on the crickets, grasshoppers, and allies (Orthoptera), including a comprehensive text on fossil crickets (Zeuner, 1939) which remains an informative resource for studying these fossils. He also published revisions and descriptions of some Late Triassic/Early Jurassic orthopterans (Zeuner, 1936, 1942), Odonata (Zeuner, 1959a), and some of the only known Jurassic beetles (Coleoptera) from Antarctica (Zeuner, 1959b). Zeuner carried out a review of the Jackson collection from the Sinemurian of Dorset (Zeuner, 1962) and although he did not describe all of the material present this remains an important text for investigating British Early Jurassic insects as many of the species currently accepted were described. Several orthopteran taxa from Britain were subsequently revised by Sharov (1968) in a book exploring the phylogeny, morphology, and evolution of the Orthopteroidea.

Paul Whalley conducted a subsequent study of the Jackson Collection (Whalley, 1985) revising some of Zeuner's earlier taxa and describing new taxa. Whalley also published several smaller studies based mostly on the Brodie collection, including descriptions of crickets (Whalley, 1982); a review of recent and fossil cicadas (Hemiptera: Cicadomorpha) (Whalley, 1983), with revisions of some of Brodie's earlier species; a review of Mesozoic moths, with a description of the oldest fossil moth from the Sinemurian of Dorset (*Archaeolepis mane*); and descriptions of lacewings and snakeflies (Raphidioptera) (Whalley, 1988). He also contributed to a study aiming to revise the true bugs and moss bugs (Hemiptera: Heteroptera) of the British Late Triassic and Early Jurassic (Popov et al., 1994).

Several important overviews of British Triassic/Jurassic insects have been published which brought together information on specific aspects of the entomofauna without offering any taxonomic revisions. The insects of the Rhaetian Penarth Group were summarised by Jarzembowski (1999) although, as he discusses, at the time there was no clear distinction between the Rhaetian Penarth beds and the Hettangian Lias beds and so the entomofaunas were described together. Several of the taxa revised in the current study were first figured as photographs here. Three of the best-known insect-bearing localities, Aust Cliff, South Gloucestershire; the Dorset coast; and Dumbleton/Alderton, Gloucestershire, were reviewed and the entomofaunas summarised by Jarzembowski and Palmer (2010). Some of the Sinemurian insects of the Dorset coast were summarised by Ross (2010), providing an important overview of the insects present and the specific horizons from which they were collected.

There have been several more recent studies summarising or revising certain taxa from the British Late Triassic/Early Jurassic insects. For example, Vršanský and Ansorge (2007) reviewed and redescribed several taxa of cockroaches, Skibińska et al. (2014) described a new true fly, and Bechly (2018) described a new dragonfly, although the latter was described from a private collection. Agnieszka Soszyńska-Maj and Wiesław Krzemiński from Poland are currently working on a project to revise the taxonomy of some Mesozoic Mecoptera and are publishing revisions and descriptions of British taxa (Soszyńska-Maj et al., 2016, 2018). There has been some interesting and important research carried out on the British Triassic/Jurassic insects but much of the material remains in need of taxonomic revision. Most of the taxa, especially the Rhaetian to Hettangian insects, are still based on historical descriptions (mostly Brodie, 1845 or Handlirsch, 1906–08).

1.2.2 Insect diversity through time: previous research

Insects are said to be rare in the fossil record, but this is not the case. Even just in the Late Triassic/Early Jurassic there are tens of thousands of insect fossils which can at least be attributed to order level, many to family, genus, or species level. This is an important resource for studying and understanding past ecosystems and will be ever more useful as the insect fossil record is refined. Researchers have been describing fossil insects for over 200 years and there are many monographs and smaller publications describing the species found in particular regions or from particular stratigraphic ages (Brodie, 1845; Scudder, 1891; Handlirsch, 1906; Bolton, 1921; Bode, 1953; Zeuner and Manning, 1976; Zherikhin, 1978; Rasnitsyn, 1985). Compilations of insect diversity through time bring together previous descriptive works and attempt to provide datasets for estimating changes in diversity through time. Although there were earlier compilations of all known fossil insect taxa (Giebel, 1856; Scudder, 1891), the first study to put together stage-level range charts of insects through time was Crowson et al. (1967) but only insect superfamilies were included. Carpenter (1992) provided genus-level descriptions of all known fossil insects for the Hexapod volumes of the *Treatise of Invertebrate Paleontology* based on literature up to 1984. The stratigraphy was not well understood at the time and so ages were only provided to period, and in some cases, epoch level, which were used to put together range charts for insect families through time.

Ross and Jarzembowski (1993) was published at around the same time but provided family data from literature up to 1991 and worked at stage level where possible, so providing higher stratigraphic resolution. Their analysis suggests an increase in family diversity across the TJB as have other studies (Labandeira and Sepkoski, 1993; Labandeira, 1994; Jarzembowski and Ross, 1996; Clapham et al., 2016), although a slight decline in family diversity was noted by Rasnitsyn and Quicke (2002). Nicholson et al. (2015) compiled a more recent family-level dataset with literature up to 2009. This study provided diversity estimates at stage level and compared the results to those of two previous datasets, namely, Ross and Jarzembowski (1993) and Labandeira (1994). Their results suggest a large

increase in diversity during the Ladinian (233 Ma) and the Carnian (223 Ma) and then a sharp decline in diversity during the Norian flattening out towards the TJB. There is little evidence for an extinction event for insects at the TJB based on any of the three datasets (Fig. 1.4). The Nicholson et al. (2015, supplement 2) dataset listed 112 and 117 insect families occurring in the Rhaetian and Hettangian, respectively, with only two families going extinct by the end of the Rhaetian.

The evidence from these previous datasets suggests that there was no major extinction event for insects at the TJB, but these were predominantly analysed at family level, except for one by Jarzembowski and Ross (1996), which was analysed at genus level based on data from Carpenter (1992), but this was of low stratigraphic resolution. It has been previously suggested that the reason for a lack of evidence for extinction events for insects at these boundaries is that the extinctions may have occurred below the family level and that analysis of lower taxonomic levels is necessary to detect an extinction signal (Ross et al., 2000; Nel and Prokop, 2009; Ponomarenko and Dmitriev, 2009; Nicholson et al., 2015). This makes sense, especially for insects which can have highly speciose and diverse families. Extinction events only significant at species level have been recorded for marine taxa (Little and Benton, 1995) and species-level turnover of certain insect taxa has been noted to occur whilst generic and family-level diversity remains constant (Rasnitsyn and Quicke, 2002). Ross et al. (2000) and Nel and Prokop (2009) suggest that species-level analysis may be required to properly analyse the end-Cretaceous mass extinction and similarly this may also be the case for detecting an extinction signal at the TJB.

Although previous studies have not detected an extinction signal for insects at the TJB it is unlikely that insects were as unaffected as previous results suggest based on the palaeoclimatological changes that occurred in the Late Triassic associated with CAMP eruptions and the effects of those changes on the palaeoecology of the British Isles. The following sections will explore the climate and ecology of the time to show that, based on this evidence, it would be expected that an extinction signal for insects should be detected in the uppermost Triassic deposits and that the reasons previous studies have not are methodological.

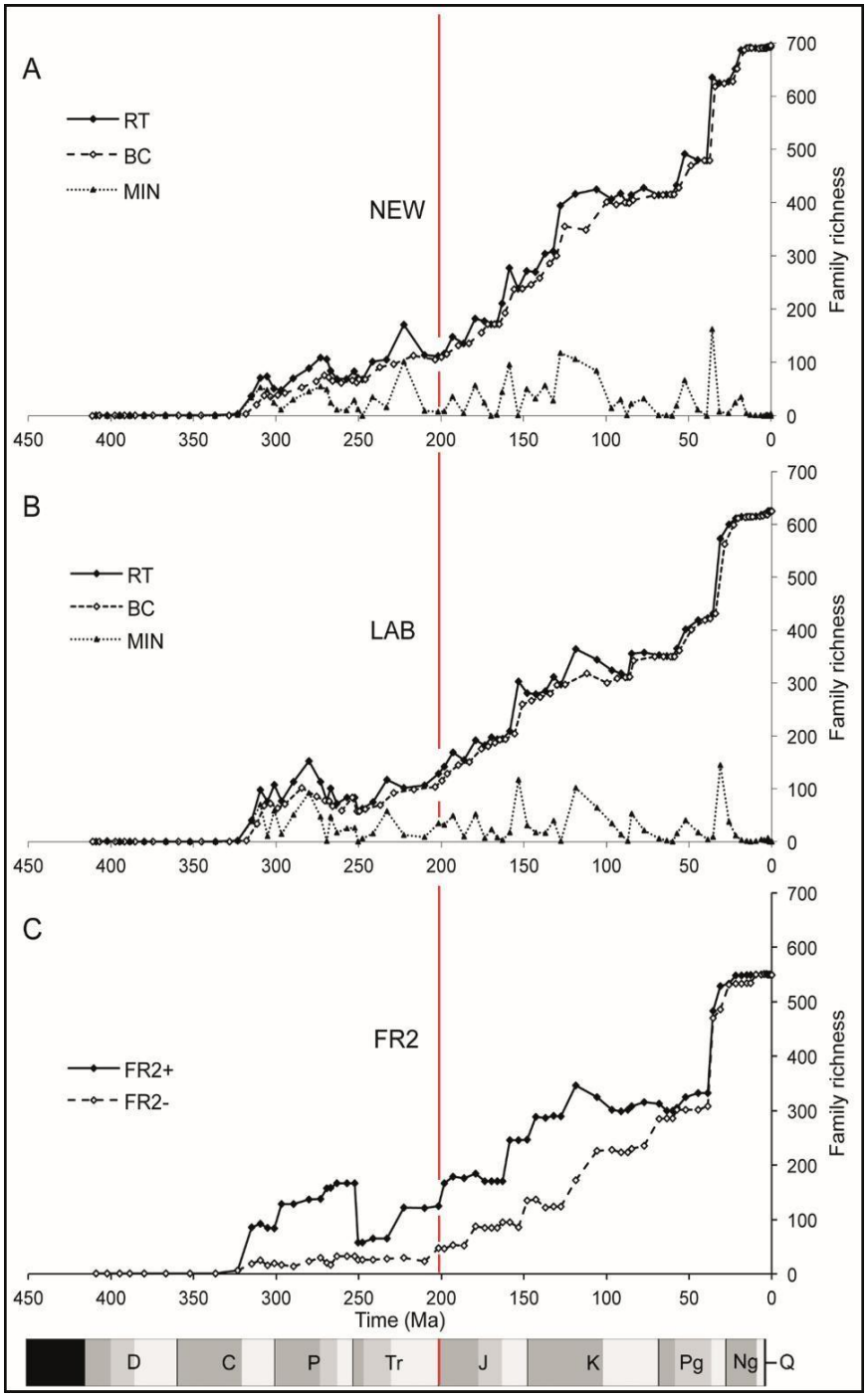

Figure 1.4. Analysis of insect family-level data through time, A. Nicholson et al., 2015; B. Labandeira, 1994; C. Ross and Jarzembowski, 1993. Modified from Nicholson et al. (2015, fig. 3).

1.3 Palaeoclimate and palaeoecology of the British Triassic/Jurassic boundary

The climate of the Late Triassic was significantly warmer than the present climate based on a lack of evidence for glaciation of the poles, climate-sensitive lithofacies, and palaeobotanical remains (Tanner, 2017). Although generally warmer, sedimentary evidence from palaeosols suggests high seasonality across broad regions of Pangaea with coastal regions experiencing a monsoonal climate

with seasonally high precipitation (Preto et al., 2010). Reconstructions by Preto et al. (2010) suggest that a persistent dry region existed to the west of the Tethys and into central Pangaea. The eastern coasts of Laurasia and Gondwana and the western coast of Pangaea were more likely to have alternate wet and dry seasons. There was a period of heightened warmth and humidity in the Middle Carnian followed by an aridification trend across much of Pangaea from the Carnian–Norian, possible due to disruption of monsoonal flow due to tectonic movement (Parrish, 1993). Sedimentary evidence, such as the transition of facies in the Newark Supergroup of the US and the Mercia Mudstone Group of the UK, suggest decreasing atmospheric moisture (Talbot et al., 1994; Ruffell and Shelton, 1999). Additionally, the presence of calcareous palaeosols and evaporites in Upper Carnian to Lower Norian sediments of Italy (Stefani et al., 2010) and the nature of the preservation of cuticles and fragmentary leaves from European Norian palaeofloral fossils (Kustatscher et al., 2017) suggest arid conditions throughout much of Europe during the Norian. This aridification trend ceased by the Rhaetian, certainly in the British Isles and the majority of the rest of Europe.

The British Rhaetian was a time of marine transgression which is evidenced by the largely terrestrial Norian Mercia Mudstone Group (red and yellow sandstones and mudstones) transitioning through periods of anoxic deeper waters (black shales) of the Westbury Formation to the shallow marine/brackish, oft marginal facies of the Lilstock Formation (white and grey limestones and blue/green marine mudstones). As the waters rose, they transgressed over the land and there was a prolonged period of land loss from the Norian, when Britain was part of a continental landmass (Coward, 1995; Thierry, 2000a), to the shallow marine, tropical archipelago of the uppermost Triassic and Early Jurassic which is discussed in further detail in Chapter 2.

The European Rhaetian Sea was a relatively stable hydrological system, marine waters continued to input from the west and a long-lasting drainage seaway to the east ensured continual movement of waters eastwards (Fischer et al., 2012). This would have affected the deposition of insects in the English Rhaetian Sea as the direction of water currents means that dead insects input into the sea would probably travel eastwards and northwards (around the London-Brabant Massif). This means that the North British Landmass (and later Scottish Landmass) is probably poorly sampled because there are very few insects from northern England, and they would not have travelled to deposition sites in the Midlands.

Although there is probably a relationship between the abundance of insects preserved and distance from land, there may not have been enough distance between these islands to make much of a difference. Deconinck et al. (2003) analysed the clay mineralogy of the Hettangian/ Sinemurian of Southwest England and considered that the clay minerals that make up the Blue Lias Formation in Dorset and Somerset could have originated on any of the islands surrounding the area, the Welsh, Cornubian, Armorican, or London-Brabant Massifs. It is thought that the islands would have been ecologically connected, because they were relatively close together, closer than Ireland is to Great

Britain today and although there were periods where some of the landmasses retreated it seems that they were never more than a few hundred kilometres from each other at most and connected by the shallow epicontinental sea for the majority of the Rhaetian and Hettangian. It would have been no trouble for strong flying insects to travel between the land masses and islands and weaker fliers could have been transported by prevailing winds.

The Westbury Formation exhibits a contradictory suite of evidence for the palaeoenvironment of the time (Allington-Jones et al., 2010). *Cruziana* is a low energy ichnofossil, in this case attributed to horseshoe crabs (Xiphosura) but is found in high-energy sandstones. These sandstones are interbedded with laminated mudstones that suggest deeper water but there are trace fossils of *Radichnus allingtona* which resembles the traces of extant fiddler crabs (species in the genus *Uca*, also known as calling crabs) which suggests emergence; however, the oldest fossil crab (*Eocarcinus praecursor*) is younger, of Pliensbachian age (Haug and Haug, 2014). Allington-Jones et al. (2010) interpret the Westbury Formation beds at Garden Cliff as being deposited under anoxic lagoonal conditions (mudstones) with episodic storms (sandstones). The ichnofauna suggests a high diversity community living in shallow marine habitats, dominated by opportunistic species colonising shallow lagoons. The dominance of opportunistic species suggests frequent disturbance, further evidence for episodic high energy storm conditions and depletion of oxygen levels. The abundance of trace fossils in sandstones but lack thereof in mudstones also suggests fluctuating oxygen levels.

The vegetation in the Westbury Formation was dominated by tetrads of *Ricciisporites tuberculatus* and *Rhaetipollis germanicus* and pollen of *Ovalipollis* and *Classopollis* (Cheirolepidiaceae) (Lindström, 2016), and also liverworts (Marchantiophyta) (Bonis and Kürschner, 2012), as inferred from the St Audrie's Bay section in Somerset, Southwest England. This locality would have been close to the Welsh and Cornubia massifs in the Rhaetian (see discussion in Chapter 2 and Fig. 2.1) and at least there is a record of the plants present on those islands. The ecological closeness of the rest of the islands is inferred from their close proximity and so would probably have had quite similar vegetation. *R. tuberculatus* is inferred to have been characterised by an herbaceous ruderal life history (Kürschner et al., 2014), which suggests periods of disturbance similar to the marine evidence previously discussed. The extinct family Cheirolepidiaceae and the extant family Cupressaceae are conifers of which *Classopollis* is found in high abundance (Lindström, 2016). Figure 1.6 provides examples of some extant relatives of the plants that made up the vegetation of the British islands of the Rhaetian Sea.

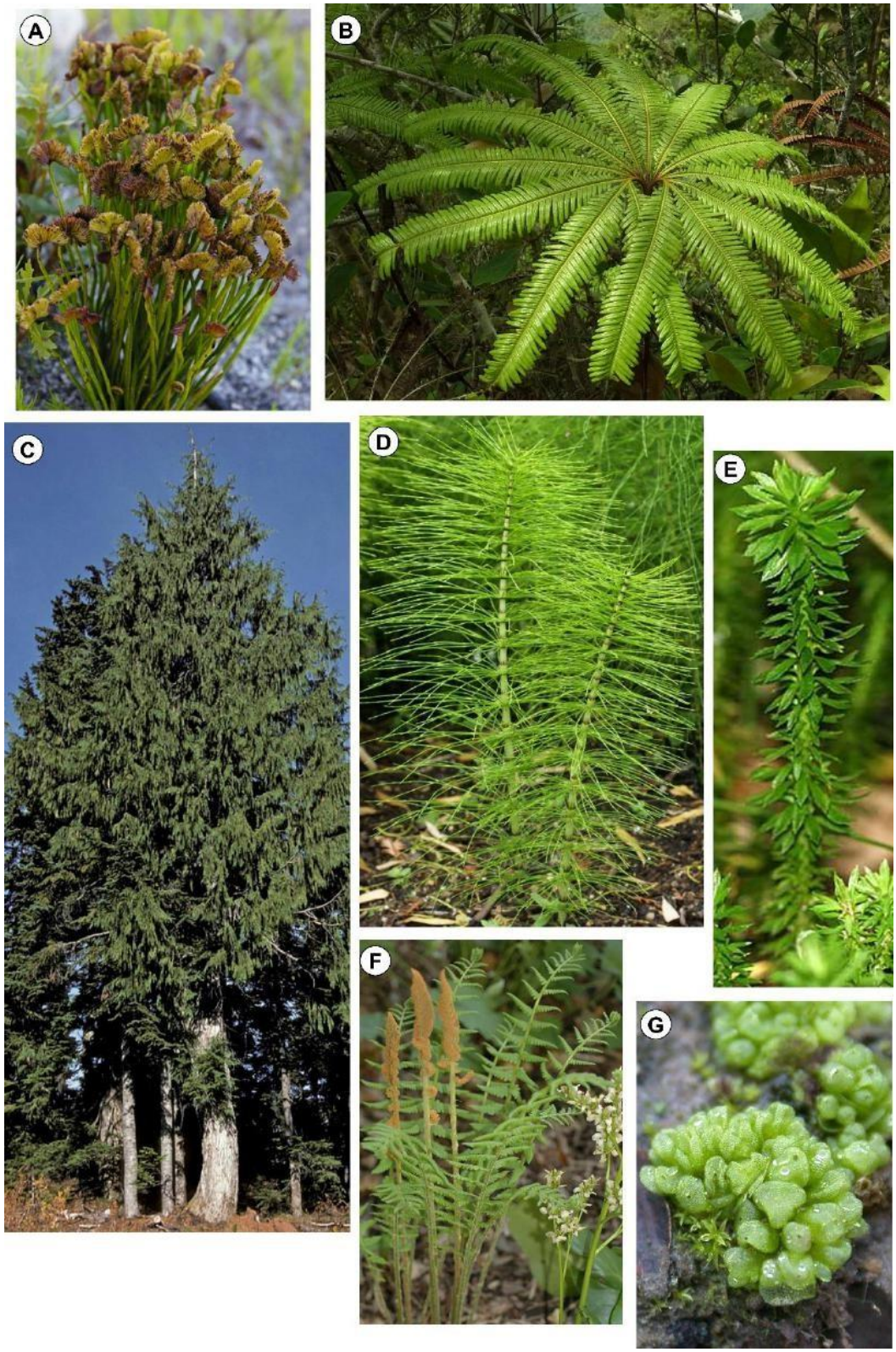

Figure 1.5. Extant examples of some of the vegetation recorded in the British Late Triassic. Ferns (A. Schizaeaceae, B. Matoniaceae); C. conifers (Cupressaceae); D. horsetails (Equisetaceae); E. spike mosses (Selaginellales), F. royal ferns (Osmundaceae), G. liverworts (Marchantiophyta). Photos taken by: Heiner Lutzeyer, Thereis Choo, Kevin C. Nixon and Jeffrey S. Pippen.

The subsequent Cotham Member is dominated by white and grey limestones with sedimentary structures such as lenticular bedding, cross-bedding, and ripple marks indicating very shallow water and high energy conditions (Mander et al., 2008). The overlying Langport Member has also been interpreted as shallow marine (Benton et al., 2002) with shallow-lagoon habitats and a broad, shallow, and relatively quiet seaway (Hounslow et al., 2004). In the Cotham Member there is an increase in spore abundance and decrease in *R. tuberculatus*, *Ovalipollis*, and *R. germanicus* in the upper part (Lindström, 2016). Bonis and Kürschner (2012) recorded different fern types, e.g. Schizaeaceae (Fig. 1.6A), Matoniaceae (Fig. 1.6B), and Osmundaceae (Fig. 1.6F) and an increase in horsetail (Equisetaceae, Fig. 1.6D), abundance. In the uppermost Cotham Member and the Langport Member the vegetation is dominated by conifers (Cheirolepidiaceae) and lesser clubmosses or spikemosses (Selaginellales, Fig. 1.6E), with abundant tree and ground ferns (Bonis and Kürschner, 2012; Lindström, 2016).

The upper Rhaetian was a time of environmental perturbation caused by CAMP eruptions, as previously discussed. Evidence from changes in stomatal index and stomatal density from the Rhaetian to Hettangian suggest a four-fold increase in atmospheric CO_2 during the Triassic/Jurassic transition (McElwain, 1999). The authors indicate that their findings agree with those from analysis of palaeosols (Yapp and Poths, 1996) but that their CO_2 estimates are more conservative. Tanner et al. (2001) calculated a much lower increase in atmospheric CO_2 across the TJB of 10% based on $\delta^{13}C$ of carbonates from palaeosols using a diffusion-reaction model. They suggest alternative hypotheses which involve an initial cooling or acidification from SO_2 release or rapid sea-level change caused by thermal doming and collapse. Guex et al. (2016) discuss this rapid change in temperatures across the TJB describing a period of 'icehouse' temperatures followed by a rise to warmer 'hothouse' temperatures across the TJB. They suggest a mechanism involving a process of gaseous release in which different gas species are released at different times during the thermal erosion of the cratonic lithosphere. SO_2 being released initially causing cold periods, switching to CO_2 release which causes warm periods. van de Schootbrugge et al. (2009) similarly suggested that climatic warming was not enough to account for the terrestrial vegetation shift they record. Instead they support a short period of cooling and acid rain caused by volcanic SO_2 fluxes.

There is evidence for major disruption to vegetation at the TJB with Lindström (2016) recording a loss of 35% taxonomic diversity at St Audrie's Bay. Positive spikes in microfloral abundance including both marine prasinophytes and terrestrial spores have been recorded in multiple sections including St. Audrie's Bay, UK (van de Schootbrugge et al., 2007); Csővár, Hungary (Götz et al., 2009); and the Newark Supergroup, US (Olsen et al., 1990). These spikes are associated with the onset of the $\delta^{13}C$ excursion of the upper Rhaetian noted previously from various global sections. This increase in microfloral activity has been explained by an increase in atmospheric CO_2. Bonis and Kürschner (2012) found evidence for a shift between different conifer species during the TJB of St

Audrie's Bay which they suggest infers the importance of relative temperature as a factor affecting vegetation extinctions. They found that in a similar section from Hochalplgraben, Germany there was rather a shift from Cheirolepidiaceae to spore-producing plants which they suggest infers a change in relative humidity. They discuss these differences as suggesting that vegetation extinctions at the TJB were not globally consistent but rather regionally variable in magnitude and composition.

Modest restructuring of vegetation was recorded in the upper Rhaetian of Britain by Lindström (2016), which related to a category IIa event of (McGhee et al., 2004). This category infers that preextinction ecosystems were disrupted to an extent that major ecological species, such as keystone species, may have been lost leading to loss of some ecosystem functionality, but that the ecosystems recovered post-extinction rather than being replaced. There is also evidence for unfavourable conditions for seed bearing plants, as there is increased abundance of spores recorded in the extinction/recovery period by van de Schootbrugge et al. (2009). Restructuring of vegetation would have a major effect on insect herbivores and their associated predators, parasites, parasitoids, and hyperparasites, especially species with specialised feeding habits. However, there is no evidence of the latter three in the Triassic from the insect fossil record. The earliest known wasps that were probably parasitic are from the Toarcian of Germany (Li et al., 2015).

The Blue Lias Formation overlies the Penarth Group and announces the Lower Jurassic. The formation consists of dark and pale mudstones and limestones often with a blue tinge to them and often highly laminated, interspersed with layers of organic-rich black shales. The British Hettangian was a time of relatively high sea level with continuing transgression, causing the complete drowning of the Welsh Massif by the Sinemurian (Thierry, 2000b; Porter et al., 2013). The climate is inferred to have been warmer and wetter than pre-TJB (Frakes and Bolton, 1992; Deconinck et al., 2003), the latter authors accepted this explanation for the patterns of clay mineralogy they recorded from the southwest and south coast of England. This pattern of heightened humidity may have persisted throughout much of the Jurassic (Jarzembowski and Palmer, 2010) although there is evidence for cold periods, e.g. in the Pliensbachian (van de Schootbrugge et al., 2005) and periods of instability with negative $\delta^{13}C$ shifts found in the Lower Toarcian (Kemp et al., 2005).

Found throughout the Early Jurassic are layers of organic-rich black shales suggesting periods of anoxia from the Hettangian Blue Lias Formation (Wignall, 2001), Sinemurian Charmouth Mudstone Formation (Simms, 2004a), and the Toarcian Whitby Mudstone Formation (Howarth, 1973) of the UK. They are also found in the Pliensbachian of Spain (Aurell et al., 2003) and Austria (Borrego et al., 1996). Toarcian black shales are also known from throughout Europe (Jenkyns and Clayton, 1986), Canada (Frebold, 1957), and Japan (Tanabe, 1983) suggesting a possible global scale anoxic period at this time (Al-Suwaidi et al., 2016). The Blue Lias Formation records a monotonous vegetation of conifers (Cheirolepidiaceae) and club mosses (Lycopodiophyta: Selaginellales), with occasionally

common pines (Pinaceae) (Bonis and Kürschner, 2012; Lindström, 2016). Davis, (2010) also suggested a sparse ground cover of the seed plants cycadeoids (Bennettitales) and horsetails, from analysis of plant fossils from the south coast of England, which would probably infer moister habitats.

An important consideration when investigating the ecological response of insects to an extinction event is the response of other closely linked taxa. Insects are intrinsically linked to plants, either as herbivores directly feeding from them or as predators feeding on those herbivores. These are complex ecological webs with layers of direct and indirect interactions that cannot always be inferred from the fossil record but in a general sense, if there is a large response from vegetation to an extinction event, then a response from insects can also be expected.

1.3.1 Insect physiological response to climate change variables

The use of contemporary studies of physiological response to changing environmental variables to inform on past periods of environmental change is not common practice and any assumptions made from such studies can only be used in a general sense, certainly when extrapolating to 200 Ma. To investigate the causes of the end Permian mass extinction Knoll et al. (2007) discussed the potential of using knowledge of the physiology of extant organisms to investigate past mass extinction events. The main aim of their study was to provide evidence for the cause of the extinction event and the authors discussed the physiological differences between different phyla of organisms as inferring variable chances of survival and re-radiation post-mass extinction.

Discussing the physiological differences between different species of insects and the effect this would have on their probability of survival would not be possible, but at a more general level physiological knowledge from current insects could be used to establish assumptions for response to periods of environmental change in the past. Especially for taxa in which the past and current species are so similar. The majority of modern orders had arisen by the end of the Triassic (Rasnitsyn and Quicke, 2002) although not all of them are represented in the British palaeoentomofauna.

Temperature is the dominant abiotic factor affecting insect herbivores with little evidence for a direct affect from rising CO_2 levels (Bale et al., 2002), although there would probably be indirect affects through the response of plants to rising CO_2 levels. This close association with environmental temperature makes sense in that insects are largely poikilothermic, meaning they are intrinsically linked to environmental temperature. Temperature may affect life-cycle duration (including rate of development), voltinism (reproductive output), population density, morphological size, extent of host plant exploitation though changes in phenology, host plant quality and nutrients available, and geographic distribution of the insect and/or of the host plant (Bale et al., 2002; Clissold and Simpson, 2015).

There are potential positive responses of insects to increased temperatures, with increased rates of development and growth and the potential for additional generations in a year leading to outbreaks

(Kambrekar et al., 2015). These changes are likely to increase insect populations in the short-term but there are complex interactions between insects and plants which are likely to negatively affect insect populations in the long-term. Increased diversity and population density of insect herbivores was recorded across the Paleocene/Eocene boundary during the Paleocene/Eocene Thermal Maximum (Currano et al., 2008). It was suggested that these increases were caused by increasing temperatures with food quality as a limiting factor. They note that the increasing groups were generally specialised feeding groups and suggested that rather than an overall increase in insect diversity that the results show an increase in the geographic ranges and diversity of specific thermophilic species, potentially following their host plants as their ranges increased.

It has also been found that synchrony between plants and insects becomes more important as environmental stress increases (Bale et al., 2002). Latitudinal and altitudinal gradients exist in which insect species can increase their dietary range as the temperature becomes less hostile. For example, the psyllid *C. groenlandica* increases the number of host plants it can feed on along a latitudinal gradient from one to four (Bale et al., 2002). Along altitudinal gradients, restraints on particular parts of a plant available for exploitation are lessened as temperature becomes more tolerant (Hodkinson, 1997). These responses, however, are not true for all species and it has been found that some, e.g. the winter moth (*Operophtera brumata*) feeding on heather, do not require tight phenological synchrony (Kerslake and Hartley, 1997) in which case the effects of rising temperature on these insect herbivores is unclear (Bale et al., 2002).

It is widely accepted that environmental stress affects specialist organisms whereas generalist organisms are more likely to survive due to their dietary flexibility. This is no different for insects, and those with specialist host plants or geographic ranges are more likely to go extinct under environmental stress. Insects are not only specialists on certain species of plant, but some are specialists on certain parts of certain species of plants. For example, certain insects are specialised to feeding on roots, leaves, stems, or galls. Each of these specialised insect herbivores will then have a community of associated predators, parasites, parasitoids, and hyperparasites. Response, therefore, also depends on life history strategies of the insect, and the host plant, growth strategies of the host plant, and the phenotypic plasticity and genotypic adaptability of host plants, insect herbivores, and their associated predators, parasites, parasitoids, and hyperparasites. For example, some insects are able to enter diapause under stressful conditions (Sgrò et al., 2016) which may reduce the impact of environmental change on insect diversity, but there are energetic costs associated with such life history strategies and so these are also a factor in the survivability of insects.

It has also been found that response to environmental stresses can vary within host plant species with distinct genotypes and that the response of associated insect food webs also varies (Barbour et al., 2016). This complicates matters further in regard to the fossil record, as it is impossible to ascertain genotypes based on fossil material, certainly not if the genotypes are morphologically identical. It is

not possible, therefore, to offer a precise assertion regarding the dynamics of diversity through past periods of environmental change, but a general understanding of the selectivity of extinctions under particular conditions of environmental change is an important piece of the puzzle for better understanding and predicting changes in extant ecosystems.

1.4 SUMMARY

The shallow marginal marine landscape of salt marshes, lagoons, and small humid islands of the Triassic/Jurassic British Isles is the setting for the extinction event under investigation. There is evidence for long-term habitat change from the Norian to the Rhaetian, from a largely arid landscape in the Norian to a much more humid environment by the Rhaetian. This change is accompanied, and encouraged, by rising sea levels, producing an archipelago of small, tropical islands by the Rhaetian dominated by lagoonal habitats and separated by a shallow, brackish/marine epicontinental sea (English Rhaetian Sea), connected to a larger epicontinental sea in the Central European Basin. These islands and lagoons were subjected to repeated transgressions and regressions of marine waters and periodic storm surges leading to a series of successive ecosystems dominated by colonising taxa, both marine (e.g. *Radichnus* traces) and terrestrial (e.g. *Ricciisporites* spores), throughout the lower Rhaetian. Transgression of water largely continued throughout the upper Rhaetian with the islands becoming smaller by the Lower Hettangian. The upper Rhaetian was a time of high energy, shallow marine habitats, similar to those of the lower Rhaetian.

Coniferous forests appear to have been the main habitat on at least the islands in the south, with tree ferns, ground ferns, club mosses, spike mosses, horsetails, and liverworts in varying relative abundances throughout the Rhaetian. Horsetails suggest watery areas such as marshes or riverine habitats and spike mosses and club mosses also usually inhabit moister habitats, such as shaded places in tropical forests; liverworts suggest damp habitats as they usually grow on damp soil or rocks. Major shifts in vegetation in the uppermost Triassic suggest an extinction event in the terrestrial realm. Although the shifting timeline of events in the Late Triassic makes timing and correlation of events difficult. The Lower Hettangian flora is impoverished compared to the Rhaetian flora with monotonous coniferous forests and club mosses with horsetails and cycadeoids returning by the Sinemurian.

Palaeoclimatological changes associated with CAMP eruptions are recorded from the uppermost Triassic, including potentially extreme fluctuations in atmospheric temperature and concentrations of SO_2 and CO_2. The evidence suggests that this led to a large-scale disruption of ecosystems, including terrestrial vegetation, from the Rhaetian to Hettangian. Increasing temperatures perhaps affected some insect populations positively in the short-term, leading to outbreaks and migrations, but long-term environmental stress, fluctuating temperatures, and the decline in plant diversity are likely to have had negative effects on insect diversity. Phenological changes in plant lifecycles and changes in geographic

distribution would have resulted from fluctuating temperatures leading to asynchrony with insect herbivores and affecting the insect's survivability in a stressed environment, indirectly leading to negative effects on insect predators, dependent upon their dietary flexibility, geographic range flexibility, behavioural flexibility, and phenotypic and genotypic plasticity.

often, it is not possible to establish specific ecological links between taxa, so it is difficult to say whether a particular predator fed upon a particular herbivore, or what the host plants were for specific herbivores. It is therefore also difficult to infer whether a species was a generalist or a specialist. Geographic ranges can be estimated from the specimens collected, which indicate whether a species is flexible geographically but does not tell us about dietary flexibility. These interactions between insects and plants exist in modern ecosystems and were probably as important in past ecosystems, albeit different, e.g. angiosperms had not evolved by the Triassic, which would mean different levels of pollination interactions, although insects were still important for gymnosperm pollen distribution. Based on our understanding of insect physiological response to rising temperatures and the record of vegetation decline across the TJB, it seems clear that there would have been an extinction event for insects in the Late Triassic.

1.5 AIMS OF THE PROJECT

The majority of the data used in this project were gleaned from historical collections of fossils that have received some taxonomic work over the years but there has been no synoptic analysis carried out since the 19th century. These collections provide some of the only insect occurrence data to bracket the TJB and if properly developed will provide an important resource for investigating the effects of environmental perturbation in the terrestrial realm through one of the largest mass extinction events in Earth history. The main aims of the current project were therefore to:

1) correlate the British insect-bearing localities to determine a series of insect horizons through the interval;

2) identify existing fossil insect collections from the interval of interest and revise taxonomy as necessary to provide a dataset of all insect occurrences across the TJB, not only first and last occurrences;

3) analyse the occurrence dataset for extinction signals in the Late Triassic at a range of geographic, stratigraphic, and taxonomic levels.

The hypothesis being that there was a major insect extinction event for insects in latest Triassic, but previous datasets could not pick it up due to the low taxonomic and stratigraphic resolution of data available at the time.

The thesis is laid out so as to provide the stratigraphic and taxonomic revisions as foundations for the later analyses. Chapter 2 provides correlations of the British historical insect-bearing strata with

each other and with well-known reference sections to better place the insect-bearing horizons in the stratigraphic succession. This is followed by a brief account of all known Late Triassic to Early Jurassic insect-bearing horizons globally. Chapter 3 provides the taxonomic revisions of British insects carried out for this study with descriptions of new and revised taxa published or in the process of publishing. This leads into Chapter 4, which is an assessment of the key assemblages across the TJB, the British Lilstock, Blue Lias, and Charmouth Mudstone formations, in terms of assemblage composition, taxonomic diversity and palaeoecology. Chapter 5 provides the results of the diversity analyses aiming to establish a record of insect diversity dynamics across the TJB at various geographic, stratigraphic, and taxonomic levels. This is finished off with a discussion on the different lines of evidence provided and what they suggest for insect diversity dynamics through the Late Triassic–Early Jurassic interval.

Chapter 2. Geological setting: Stratigraphy of global insect bearing horizons

Part 1. Correlating the Penarth and Lias insect limestones of Britain

The River Severn is the longest river in Britain. Sourcing from the Cambrian Mountains in mid-Wales it flows into the English Midlands, heading south west to deposit into the Bristol Channel, which forms the north coast of Somerset and the south coast of Wales, both well known for their Late Triassic and Early Jurassic research. The Severn Valley, cut by the river into the English Midlands and South West, is the most productive area in the world for insects from around the Triassic/Jurassic boundary (TJB). This valley was the 19th century setting for the excursions of Victorian naturalists that lead to the large collections of fossil insects we have today. The River Severn offers some spectacular cliffs along its estuary and through the valley, but they are not always accessible and are not always the most fossiliferous. Many of the insects in the collections are from long abandoned quarries or pits, or from railway or road cuttings. The early to mid-19th century saw several railway companies being founded in the region with railway lines running through the Severn Valley by the 1840s, which provided temporary exposures of insect-bearing beds from the Rhaetian and Hettangian.

"Insect Limestone" was a term coined by Brodie to describe what he considered to be a continuous but laterally variable series of limestone beds in the "Lower Lias". At the time the Lower Lias was generally considered to be anything between the Tea Green Marls of the Westbury Formation and the Planorbis Zone of the Blue Lias Formation. The "Insect Limestone" was considered to be a continuous horizon based on lithological and biological similarities between different areas (Brodie, 1845). It is clear however that this is not the case and it was pointed out quite early that the Insect Limestone proper, as initially identified by Brodie, in Worcestershire and Gloucestershire was found below the lowest beds of the Lias and is therefore "Rhaetic" (Woodward, 1893; Richardson, 1903; Old et al., 1991). "Rhaetic" was a lithostratigraphic term for the rocks below the Lias Group but was often considered to sit between the Triassic and Jurassic (Richardson and Trueman, 1929). In current nomenclature, this rock unit is known as the Penarth Group, which corresponds with the chronostratigraphic Rhaetian stage.

The Insect Limestone proper is a hard, blue/grey limestone with buff coloured bands, often laminated, but featureless when compared with the lower Cotham limestones. Brodie (1858), whilst discussing sections at Wainlode and Garden cliffs in Gloucestershire, described the Insect Limestone near the summit as laminated, but very hard when not weathered. He says that this was overlain with "10 inches" (~25 cm) of yellow shale and another very distinctive bed, very hard, very blue and containing an abundance of oysters known as "*Ostrea*", now classified as Ostreoida: Osteridae: *Liostrea*, the most common species being *L. hisingeri* (Nilsson, 1832), previously *O. liassica* and

mussels known as "*Modiola*", which are classified as Mytiloida: Mytilidae: *Modiolus*. This bed is usually known as the "basement bed", or "*Ostrea* bed" (Brodie, 1845; Woodward, 1893) and generally marks the lower boundary of the Blue Lias Formation: Wilmcote Limestone Member (Old et al., 1991). The stratigraphy of the British Lias is relatively well researched, and specific horizons can be pinned down to a high-resolution age, often to an ammonite zone or subzone. The Penarth Group is more difficult; the lack of ammonites makes correlations with international standards difficult and frequent disconformities caused by erosion or non-deposition resulted in hiatuses in the sedimentary succession. There are also issues with the placement of the pre-planorbis beds (lowermost Lias Group), certainly in the Severn Valley where the Langport Member (=White Lias) is absent and it can be difficult to precisely identify where the Cotham mudstones become Lias mudstones.

2.1 Materials and methods

A list of Late Triassic–Early Jurassic insect-bearing beds was compiled from museum collections and the historical literature. The lithology and biological content of the different beds was noted. Sections were prepared from the original publication reporting insect fossils and refined where possible using more recent observations. As there were numerous exposed sections at the time it was important to use the original insect-reporting paper as the starting point, otherwise the sections could represent different pits exposing a different part of the sequence. Composite sections were prepared for distinct areas of the Severn Valley: Estuary and Bristol area, Vale of Gloucester, Vale of Evesham; and the Devon Coast for comparisons.

Field work was carried out at several localities still exposing insect-bearing strata; firstly, to find the insect-bearing beds in situ and determine their stratigraphic position. Secondly, to determine whether it was feasible to carry out a period of field collection, particularly in the few localities which offered insect-bearing horizons in both the Triassic and Jurassic. Localities were as follows: Aust Cliff (ST 565 895–ST 572 901) in South Gloucestershire, a cliff section on the banks of the Severn Estuary and a popular locality for palaeontological field work; Wainlode Cliff (SO 845 257) in Gloucestershire, a smaller cliff further up the Severn River, which, although being less well-known, has produced many more insects than Aust Cliff; the Penarth cliffs (ST 190 702) on the banks of Cardiff Bay, insects have not been collected from this locality but it is the type section for the Penarth Group; Sedbury Cliff (ST 5578 9338) is another cliff section on the banks of the Severn Estuary, on the opposite side to Aust Cliff; and several localities along the Dorset Coast including Stonebarrow (SY 371 929), Black Ven (SY 356 930), Monmouth Beach (SY 333 914), and Pinhay Bay (SY 318 908). The type section for the Wilmcote Limestone Member of the Lias Group is at Wilmcote Quarry (SP 151 594) and a reference section at Temple Grafton (SP 121 539) in Warwickshire. Many of the insects in the collection were from this area but it is not clear where precisely the historical sections were located, and the current quarries are considered to expose beds stratigraphically higher than the

insect beds of yore (Radley, 2003). It is possible to lithologically correlate the limestones of the Penarth and Lias groups, but only over short distances. Facies can change rapidly, certainly in the heavily faulted TJB of the area. An in-depth literature review, coupled with the field work, and a lithological assessment of the museum specimens allowed for the correlation of insect-bearing limestones between the historical sections, and with better studied contemporaneous sections. St Audrie's Bay was a candidate for the base of the Jurassic GSSP and as such is a very well-studied reference section for the TJB.

2.2 RESULTS

There are 66 localities in the UK from which insects have been recorded from Upper Triassic/ Lower Jurassic (Fig. 2.1) rocks. of these localities, 34 were upper Rhaetian, 15 were Lower Hettangian, five were Sinemurian (three both lower and upper; two only lower), one Pliensbachian, and 13 Lower Toarcian. The main focus of the project is on the TJB, so the Rhaetian, Hettangian, and Sinemurian faunas are discussed primarily, but the Toarcian data are also included in the dataset and so are discussed briefly. There are at least two distinct series of Brodie's insect-bearing limestone, one in the Penarth Group: Lilstock Formation and one in the Lias Group: Blue Lias Formation (Figs 2.2 and 2.3). A few additional fossils were recorded from the black shales of the Westbury Formation and the pre-planorbis beds. A younger series of beds with insect-bearing limestone nodules is found in the Charmouth Mudstone Formation of the Dorset Coast (Sinemurian). One horizon of insect-bearing limestone exists in the Lower Toarcian, from the Whitby Mudstone Formation in the north and the Beacon Limestone Formation in the south. It appears to be contemporaneous with the very productive beds from Germany.

2.2.1 Penarth Group

The Penarth Group consists of the lower Westbury Formation overlaid by the Lilstock Formation (Swift and Martill, 1999; Benton et al., 2002). The base of the Westbury Formation is marked by the fossil-rich Rhaetic Bone Bed, overlying the blue/green-coloured mudstones of the Blue Anchor Formation. Above the basal Bone Bed, the Westbury Formation comprises a short series of alternating dark shales and sandstones with clasts of Blue Anchor rocks embedded in the shales and ripple marks in the sandstones suggesting a shallow environment with strong winds and at least relatively coastal, with winds or storms strong enough to break off pieces of the Blue Anchor land and deposit them in the Westbury Formation forming sediments. Succeeding this are thicker layers of black shales, usually laminated and often quite fossiliferous, and the *Pecten* beds (lower and upper). They comprise dark grey, hard, shelly (*Pecten* scallops), sandy biosparite with quartz pebbles and dark greenish shales. The thick layer of dark shale that overlies them contains sand lenticles in the lower part.

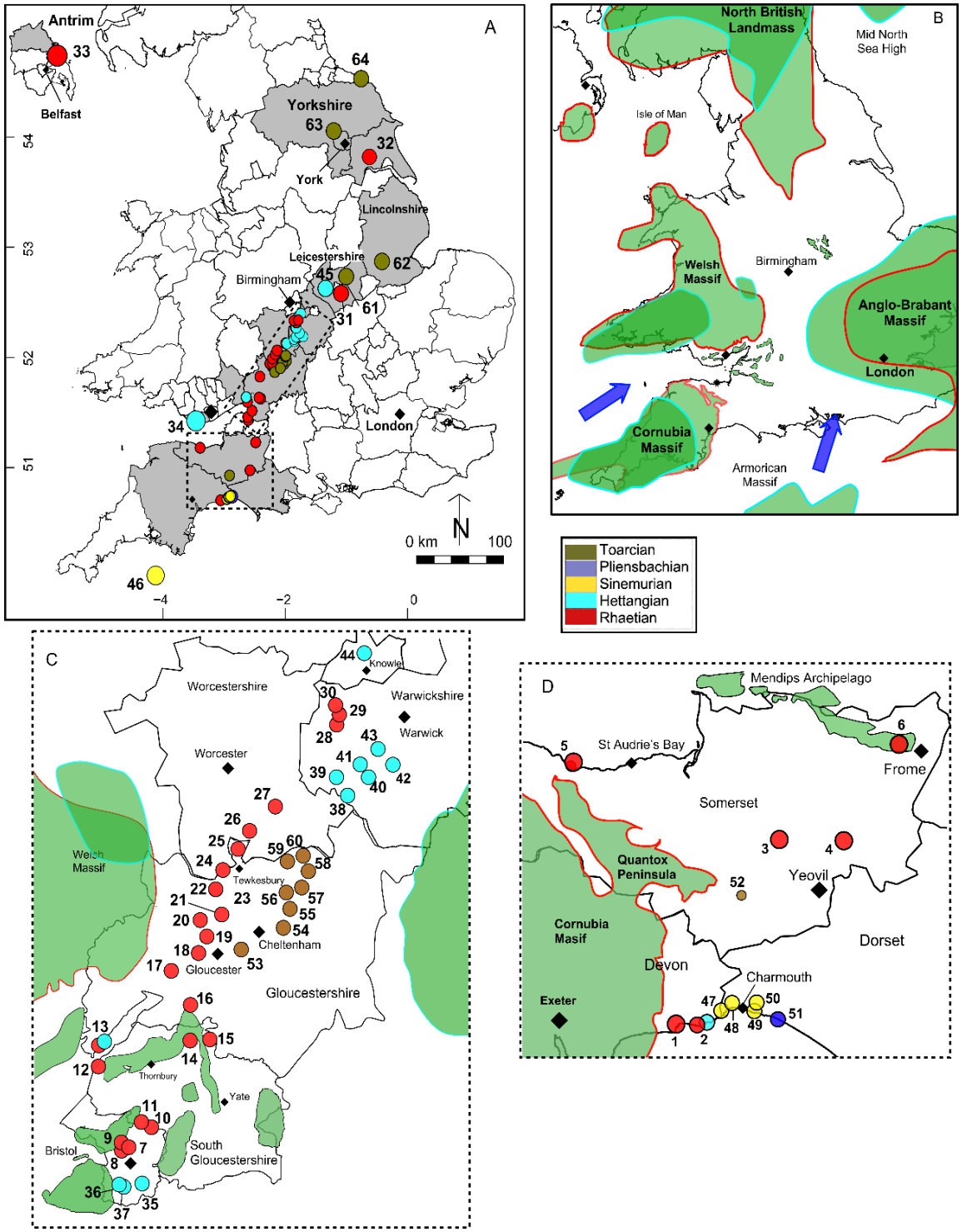

Figure 2.1. Insect-bearing localities from Britain. A. All localities coloured by age with insect-bearing counties shaded in grey. B. Palaeogeographic reconstruction of the Rhaetian and Hettangian; estimated Rhaetian coastlines in red, Hettangian coastlines in Blue. C. Severn Valley. D. Somerset and Dorset Coast. Localities: 1. Culverhole Point, 2. Pinhay Bay, 3. Camel Hill, 4. Langport, 5. Blue Anchor, 6. Holwell, 7. Cotham, 8. Redland, 9. Clifton, 10&11. Stoke Gifford, 12. Aust Cliff, 13. Sedbury Cliff, 14. Cromhall, 15. Charfield, 16. Tortworth, 17. Garden Cliff, 18. Highnam, 19. Prior's Norton, 20. Ashelworth, 21. Wainlode, 22. Hasfield, 23. Grey Hill, 24. Forthampton, 25. Brockeridge, 26. Strensham, 27. Cracombe, 28. Shellfield, 29. Stooper's Wood, 30. Brown's Wood, 31. Glen Parva, 32. Hotham (East Riding of Yorkshire), 33. Whitehead, 34. Cnap Twt, 35. Bedminster, 36. Nubbers, 37. Locks Mill, 38. Bickmarsh, 39. Bidford, 40. Binton, 41. Temple Grafton, 42. Stratford-on-Avon, 43. Wilmcote, 44. Copt Heath, 45. Barrow-upon-Soar, 46. Western English Channel, 47. Monmouth Beach, 48. Black Ven, 49. Stonebarrow, 50. Catherston Lane, 51. Golden Cap, 52. Ilminster, 53. Churchdown Hill, 54. Strutfield Wood, 55. Cleeve Hill, 56. Nottingham Hill, 57. Gretton, 58. Nuneaton Farm, 59. Alderton Hill, 60. Dumbleton pit, 61. Tilton-on-the-Hill, 62. Spittlegate, 63. Skelton, 64. Rosebury Pyke.

Insects have been collected from several layers in this part of the Westbury Formation from Stoke Gifford, South Gloucestershire (ST 619 800) and Cotham Road, Bristol (Short, 1904) (ST 584 739). At Stoke Gifford, one layer was described as a grey laminated marl, with mica-flakes and thickly bedded siliceous layers at the base and ripple markings and the other bed as a greenish-black calcareous shale producing abundant *Pecten* and “many elytra of beetles and wings of insects", which were often pyritized. The Stoke Gifford insects examined, however, were from the Brodie collection and were embedded in a hard, blue/grey limestone typical of the younger beds. From Cotham Road, Short reported some pyritized elytra of beetles from a black shale below the *Pecten* bed. There is also one insect reported from a layer of black shale less than 1 m above the bone bed at Glen Parva, Leicestershire (Horwood, 1916).

Overlying the Westbury Formation is the Lilstock Formation, comprising the Cotham Member followed by the Langport Member. There is an abrupt change in lithology from the black shales of the Westbury Formation to the light grey/green calcareous mudstones of the lower Cotham Member. The upper Cotham Member comprises a laterally variable series of limestones alternating with the grey/green mudstones and it is here that most of the Penarth insects are found. At its full extent, the Cotham Marble series consists of seven limestone horizons (Short, 1903; Benton et al., 2002) including the distinctive Landscape Marble of the Bristol area, which is formed from microbialite structures representing microbial deposits in marginal waters.

The Bristol area consisted of archipelagos of small islands at the time (Fig. 2.1), as evidenced by the numerous fissures in Carboniferous rocks filled with Upper Triassic sediments representing karstic cave systems (Whiteside and Marshall, 2008; Mears et al., 2016; Morton et al., 2017). Exposed land affects sedimentation processes and facies development, which affects the probability of preservation, certainly for the more delicate fossils such as insects. There were fewer insects collected from the Rhaetian rocks of the Bristol area, despite being specifically searched for (Brodie, 1845; Moore, 1867; Short, 1904). This could represent a post-depositional bias, in that the reduction in lamination in the limestones of the Bristol region affected the probability of deposited insects being preserved. Alternatively, it could represent a depositional bias, in that the position of the islands cut off the Bristol lagoon from most of the runoff water from the larger Welsh Massif reducing the number of insects deposited in this area.

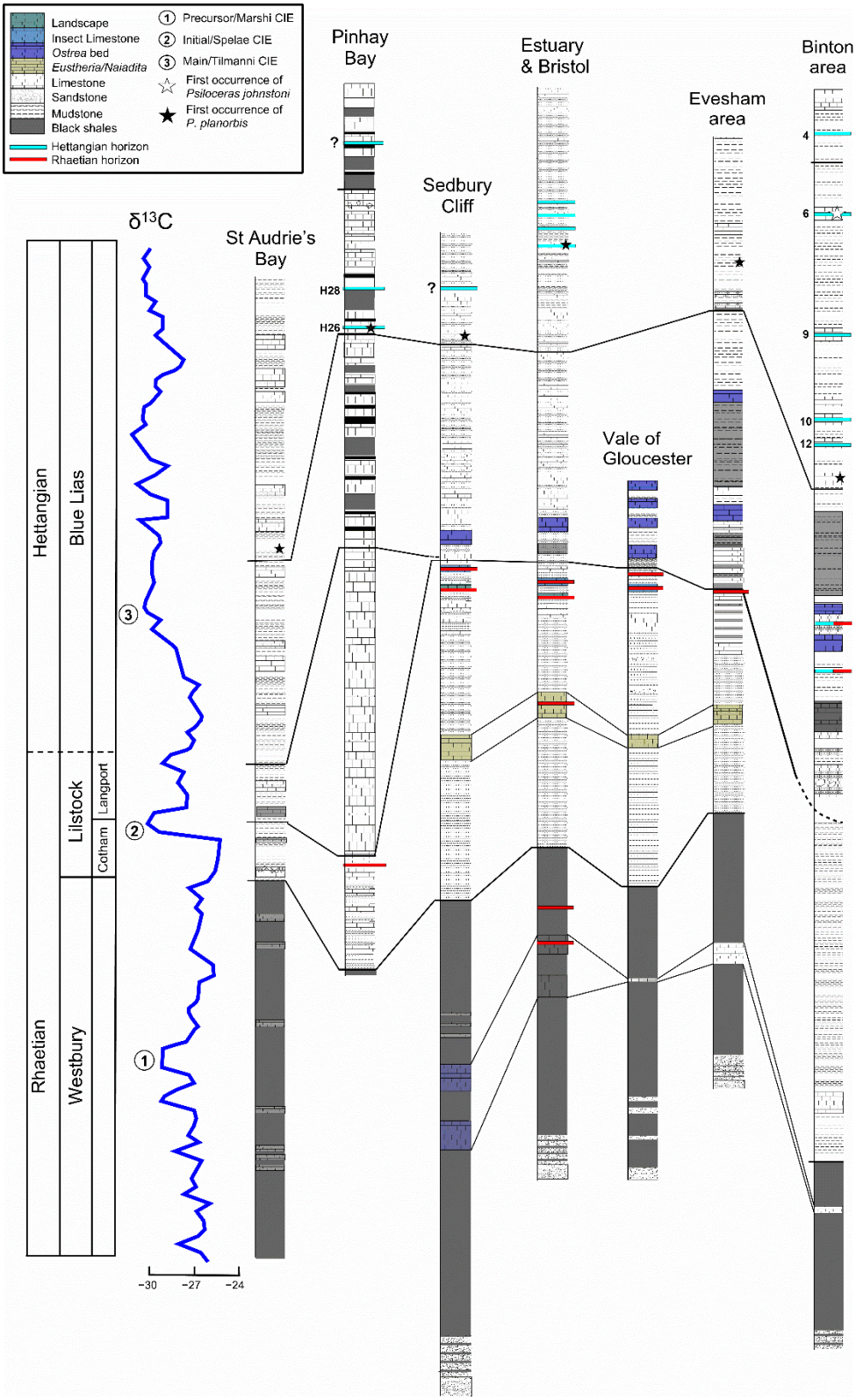

Figure 2.2. Correlation of Late Triassic/Early Jurassic insect-bearing horizons (coloured as in Fig. 2.1) with the St Audrie's Bay reference section (modified from Hesselbo et al., 2002). Pinhay Bay (modified from Page, 2002, p. 295; Korneisel et al., 2015, p. 132) Sedbury Cliff (based on Richardson, 1903, p. 396; Welch and Trotter, 1961, p. 120); Estuary & Bristol (based on Brodie, 1845; Moore, 1867; Short, 1904; Green et al., 1992); Vale of Gloucester (based on Brodie, 1843, 9. 16, 1845; Richardson, 1903; Benton et al., 2002); Evesham area (from Brodie, 1845; Murchison, 1845; Ambrose, 2001); Binton area (after Brodie, 1845; Wright, 1860; Tomes, 1878).

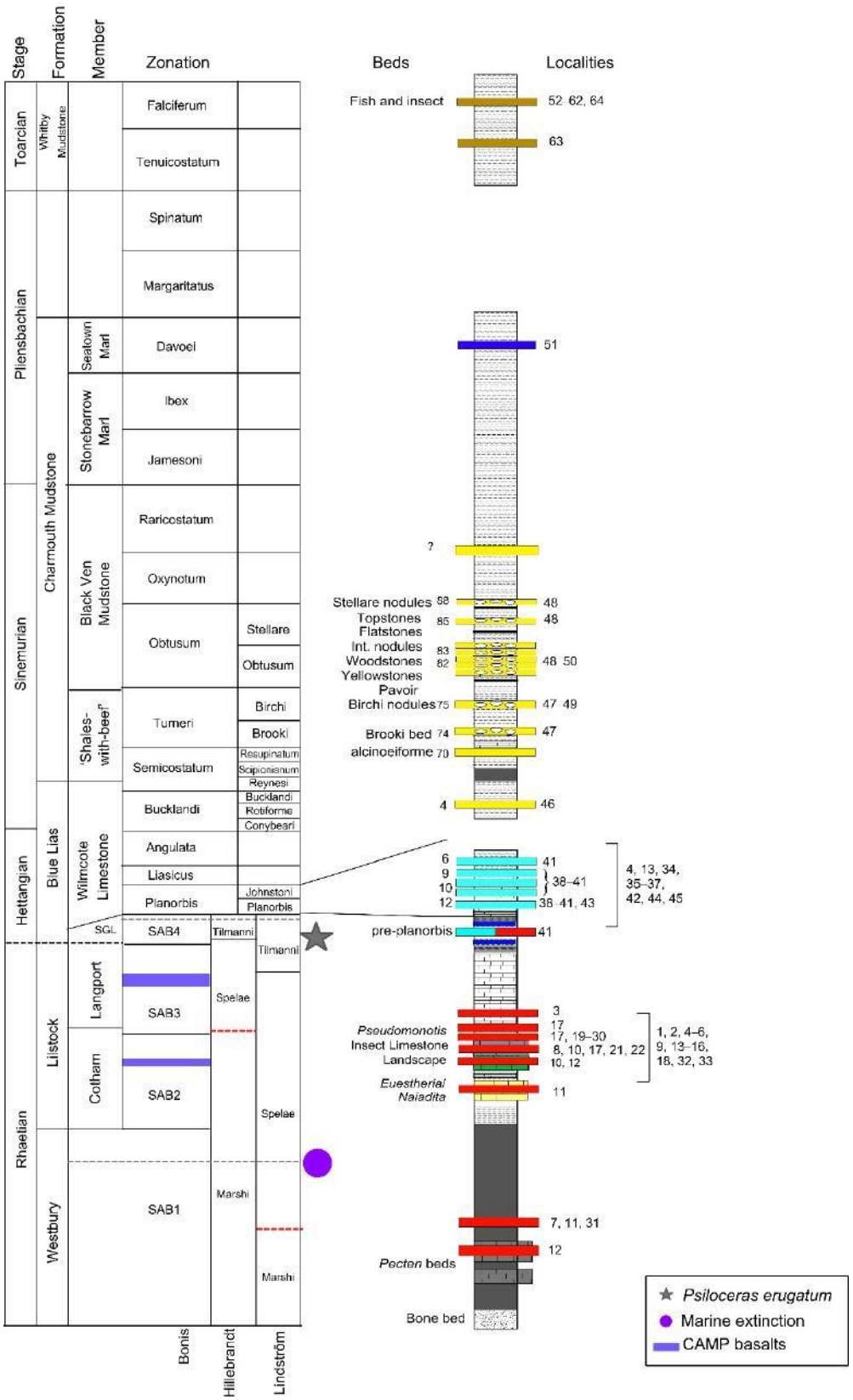

Figure 2.3. Stratigraphy of British insect-bearing horizons. Sections from Figure 2.2 merged into one column, also including Sinemurian and Toarcian horizons (Fig. 2.1 for colours). Red dashed line for onset of ETE included at both proposed positions (Hillebrandt et al., 2013; Lindström et al., 2017); also, informal

palynological zones for the Rhaetian (Bonis et al., 2010). Localities besides the brackets are of unsure horizon within the range indicated. Horizon colours as per those in Figure 2.1.

The Insect Limestone proper is represented by a bed of hard blue/grey compact limestone with buff coloured bands and often gypsum veins towards the top of the Cotham Member, but can be quite variable (Fig. 2.4). It is not as rich in shells as the overlying pre-planorbis "shelly limestones", but mussels and oysters are known. It has variously been considered to be part of the pre-planorbis beds (Wright, 1860; Simms, 2004a), part of an attenuated Langport Member (Richardson, 1904; Swift and Martill, 1999), or part of the top beds of the Cotham Member (Benton et al., 2002). Mayall and Wright (2015) discussed a prevalent band of limestone at the top of the Cotham Member as a hard, blue-grey micrite, 5–15 cm thick with cm-scale blue to grey colour banding and silt beds 1–2 cm thick. A similar bed was mentioned by Allard et al. (2015) at Manor Farm, not far from Aust Cliff as a *Modiolus*-rich biomicrite which passes laterally into typical stromatolitic Cotham Marble lithologies. Whilst discussing the river/estuary cliff sections at Aust (ST 565 895) and Sedbury (=Sudbury) (ST 554 929), Brodie (1845 p. 82) mentioned that the Insect Limestone was absent at Aust and that insects were only found in the Landscape Marble (=Landscape Stone) of the Cotham Marble series. At Sedbury, however, he described two distinct limestone beds at the east of the cliff, the Insect Limestone and the Landscape Marble, "blending" towards the west of the cliff to form a seemingly single bed. The Landscape Marble has not produced as many insects as the Insect Limestone, but many of those from Aust Cliff are well preserved (Jarzembowski and Palmer, 2010; Kelly et al., 2018a), and often form amalgamated masses of beetles and wings (Fig. 2.5).

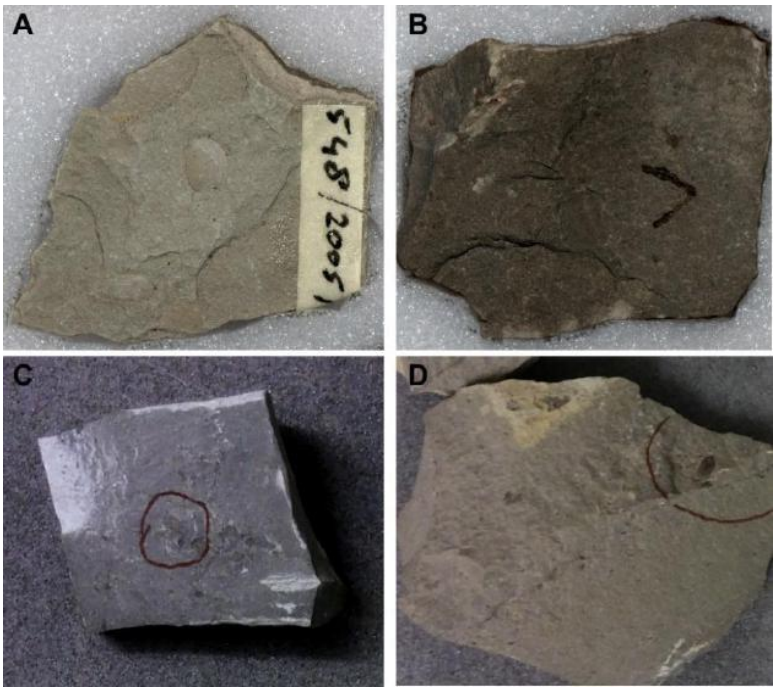

Figure 2.4. Four specimens from the Insect Limestone at Wainlode. A) 548/2005/2 and B) 548/2005/3 from the Brodie collection at the Royal Albert Memorial Museum, Exeter; C) CC 3216 and D) CC 3214 from the Simms collection at Bristol Museum (c. 1990s).

Figure 2.5. Mass of beetles and wings from the Landscape Marble of Aust Cliff (YM816), from the Brodie collection at Yorkshire Museum (Brodie, 1845, pl. 9, fig. 9).

In many localities in the Severn Valley the Insect Limestone lies within in yellow/brown calcareous mudstones, typical of the Cotham Member locally (Richardson, 1903; Barclay et al., 1997). (Brodie, 1843) described the limestone lightening to an almost white colour and becoming richer in shells as it passes upwards into this shale. In the Vale of Gloucester and Evesham areas, Brodie (1845) describes a laterally discontinuous, softer and whiter limestone bed containing insects passing down into the typical hard, blue Insect Limestone and overlaid by a layer of shale then the *Ostrea* beds. The white limestone does not always repose directly on the Insect Limestone as they are sometimes separated by a thin layer of laminated brown calcareous shale (Richardson, 1903, p.172), typical of the Cotham Member locally (Barclay et al., 1997). Richardson referred to the Insect Limestone, including this upper creamy-white limestone horizon, as the *Pseudomonotis* bed, as it was particularly abundant in the scallop *Pseudomonotis*, (revised to Pectinoida: Oxytomidae: *Oxytoma*) and he considered it to be an attenuated form of the White Lias (Langport Member). Swift (1995) also discusses the extent of the White Lias in the area and considered Richardson's *Pseudomonotis* Bed (i.e. Brodie's Insect Limestone) to represent an attenuated Langport Member in the area. It is generally considered to be either Langport or Lias, as it has characteristics of both (Cox et al., 1999). A discontinuous limestone at the base of the Langport Member has also been reported by Old et al. (1991) and Benton et al. (2002).

This bed could represent the remnants of an eroded Langport Member, or it could be the top of the Cotham Member. The division between these units is far from clear in the area, as the browny mudstones of the Cotham Member and the greyer mudstones of the Wilmcote Limestone Member weather similarly (Barclay et al., 1997). However, both beds underlie the pre-planorbis beds including the distinctive *Ostrea* bed, which allows them to be correlated with other Rhaetian-aged beds. Besides,

whether they are Cotham or Langport they occupy a similar position in the upper Rhaetian within SAB3 of Bonis et al. (2010), in the uppermost Marshi Zone as considered by Hillebrandt et al. (2013) and Zaffani et al. (2018), or in the upper part of the Spelae Zone as defined by Lindström et al. (2017) (Fig. 2.3).

Below the Insect Limestone and the Landscape Marble is a yellow/grey-blue passing laterally into paler yellow/white/grey limestone, sometimes with a nodular and dendritic upper bed with irregular fractures (Brodie, 1845; Benton et al., 2002). It is usually surrounded by thick layers of green/grey mudstones and comprises a series of alternating thin limestone and mudstone horizons (Welch and Trotter, 1961). It has been referred to by several names, including the *Cypris* and Plant Bed (Brodie, 1845, etc) and the *Estheria* Bed or *Cypris* Bed (Richardson, 1903). The mudstone layers are abundant in shells, including the common Rhaetian ostracod *Euestheria* (=*Estheria*) (Morton et al., 2017) and the limestone horizons are abundant in freshwater liverworts such as *Naiadita* and *Hepaticites* characteristic of the Rhaetian (Buckman, 1850; van Konijnenburg-van Cittert, 2008). Several layers have produced insects but in much fewer numbers than the other limestones discussed (Short, 1904; Harris, 1938). This bed is often associated with the Insect Limestone and is a good marker for the Cotham Member when the Landscape Marble peters out towards the north, as it extends over a much larger area (Harris, 1938).

Severn Valley: Vale of Gloucester.—The Cotham Marble changes from the Bristol area into the Severn Valley, becoming a hard, fissile limestone, with abundant scallops (Green et al., 1992). The marginal, very shallow lagoon facies of the Bristol area pass laterally into slightly deeper, less perturbed sediments, with better lamination. Into the Vale of Gloucester, the Cotham Marble series passes into more fissile, structureless limestones and insect remains become more prevalent. This increase in insects could be due to the increase in lamination, leading to higher probability of insect preservation, or it could be due to the position of area, north of the Bristol islands. The Vale of Gloucester was just off the coast of the Welsh Massif (Fig. 2.1) and there was evidently fluvial input from this island into the Rhaetian Sea, potentially from this coast. There are beds abundant in insects and terrestrial or freshwater plants, often found together with freshwater/brackish crustaceans and brackish/marine shells. The insects preserved are generally not littoral and the vast majority of insects cannot live in marine or brackish environments which suggests that they were transported from the more interior of the island by streams or rivers, were blown out into the water, or for the stronger flyers, died on the wing over the water.

At Garden Cliff, Westbury-on-Severn (SO 717 129), insects are found in two beds, the Insect Limestone and the *Pseudomonotis* bed, which is locally extremely shelly (Fig. 2.6), much more so than the insect-bearing limestone at any other locality. These beds are traced northwards and although not as shelly both beds were reported from near Hill Farm, Hasfield (SO 825 276) by Brodie (1845, p. 62)

and (Richardson, 1903, p. 172). The upper bed is described as soft, whitish and rich in shells and the lower one the hard, blue Insect Limestone which weathers light brown, a character seen in the more northern sections also. Here, the *Ostrea* bed was reported in situ above the insect beds. The *Euestheria*/*Naiadita* bed was not exposed here but it was at the nearby sections at Wainlode Cliff (Benton et al., 2002) and Coomb Hill (Brodie, 1845; Richardson, 1903, p. 175), with the Rhaetian liverwort *Naiadita lancelota* and ostracod *Euestheria brodiana*. Wainlode Cliff (SO 845 257) has been particularly abundant for insects, historically (Brodie, 1845, p. 58) and recently (Jarzembowski collection at NHMUK; Simms collections at BRSMG). The section is relatively well studied as it is a river cliff and thus, still accessible (Richardson, 1905; Benton et al., 2002, p. 429; p. 235).

Figure 2.6. Insect-bearing limestone from Garden Cliff with abundant *Oxytoma* ("*Pseudomonotis*") scallop shells (NHMUK 10808).

Grey Hill, Apperley (SO 852 270) represents a Penarth outlier (Worssam et al., 1989) and has been quite productive for insects (Brodie, 1845; Richardson, 1903a, p. 140). The specific section visited by Brodie was overgrown when Richardson visited, so the exact position is difficult to ascertain, but "Brodie's Insect Limestone" was described as lying in the *Pseudomonotis* bed, closely associated with the *Euestheria*/*Naiadita* Bed. Insects were reported from the Insect Limestone of Ashelworth (SO 812 255; Brodie, 1845, p. 63), although no insects from this locality are in the collections, and Forthampton (SO 856 326) (Brodie, 1845, p. 66) and are reported to underlie two or three bands of the *Ostrea* beds. At Forthampton the Insect Limestone exhibits its usual hard, blue lithology underlaying brown laminated shales at the lower end of the quarry. At the other end Brodie describes a similar bed of hard, blue limestone passing into the aforementioned softer, white limestone underlying the *Ostrea* bed, and considers them to be the same bed, dislocated by a fault. No specific section was offered by Brodie for the path cutting at Prior's Norton (SO 866 245), but he did describe the beds as similar to

the other sections locally (Brodie, 1858) and so it probably does not correspond with the black shale section of the Westbury Formation described from Prior's Norton by Richardson (1903a, p. 141).

Severn Valley: Evesham area.—Strensham quarry (Brodie, 1845, p.70) is situated in the middle of a line of quarries running from Brockeridge Common (Brodie, 1845, p.67) to Defford Common (section of Bourne Bank, Richardson, 1903a, p.152) (SO 893 377– SO 918 432). The Insect limestone was described similarly to that at Forthampton (SO 856 326), a generally blue hard limestone passing into a softer white limestone at the same position as at Brockeridge, Coomb Hill (SO 893 295), and Bushley (SO 898 307), although there are no insects from the latter two in the collections. At Coomb Hill the Insect Limestone is associated with the *Euestheria*/*Naiadita* bed within layers of brown and yellow mudstones overlaying the black laminated mudstones of the Westbury Formation (Murchison, 1845, p.47), exactly corresponding to the sequence at Wainlode Cliff. At Strensham, the Insect Limestone underlies brown/black shales, within a series of blue shales and hard limestones described as similar to those of the Cotham Member of Bristol and overlying black shales as at Wainlode and Garden cliffs. The limestone is generally white or grey/blue sometimes weathering to brown (Fig. 2.7), as described from Hasfield. These beds underlie the *Ostrea* bed, as pointed out by Woodward (1893) who stated that they were, therefore, "Rhaetic" and not associated with the insect limestones in Warwickshire.

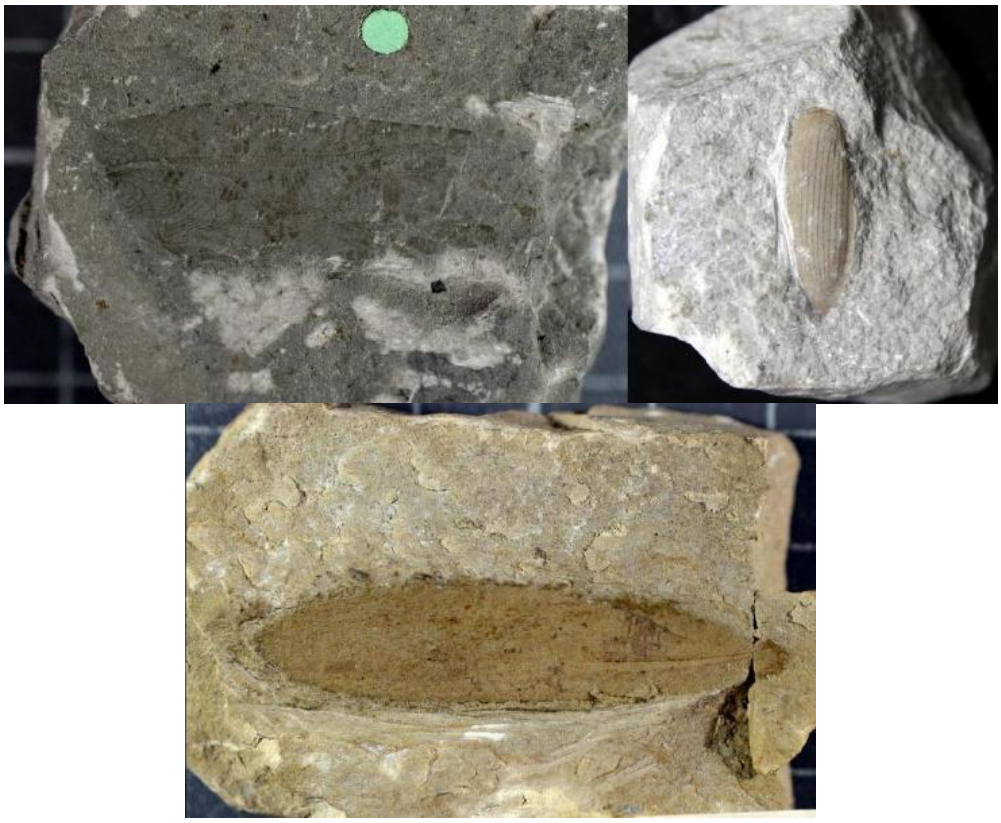

Figure 2.7. Insect-bearing lithology of Strensham. Clockwise from top left: NHMUK I.10535; I.10700; I.10531.

The insect-bearing limestones at Strensham, however, are considered to lie in the Stock Green Limestone (pre-planorbis beds) of the Wilmcote Limestone Member (Worssam et al., 1989; Barclay et al., 1997; Ambrose, 2001). The division between this member and the underlying Cotham Member is unclear given the similarity in the mudstones when weathered (Barclay et al., 1997). The descriptions of the insect-bearing limestones at Strensham and Brockeridge are remarkably similar to those for the Insect Limestone from the Vale of Gloucester, a hard, blue limestone within a series of blue/brown calcareous shales passing into a discontinuous softer white limestone (possibly the attenuated Langport Member). It is possible, therefore, that the insect-bearing beds here are continuous with those of the Vale of Gloucester, laying below an eroded Langport Member in places (e.g. the western part of the pit at Strensham, Brodie, 1845) or directly below the Stock Green Limestone (pre-planorbis beds) of the Wilmcote Limestone Member where the White Lias is absent. Towards the north of the Severn Valley, Penarth/Lias outliers are found in north west Warwickshire in the Redditch area (Old et al., 1991). They are known as Brown's Wood (SP 114 643), Stooper's Wood (SP 124 635), and Shelfield (SP 116 619) (Brodie, 1865, 1874, 1886). Although a section was never exposed with the insect-bearing bed in situ, the blocks of loose limestone containing insects were described as hard, compact, crystalline and associated with *Euestheria*. The *Euestheria* from Brown's Wood have recently been reassessed and the beds containing them aged as Rhaetian (Morton et al., 2017). The White Lias is mostly absent from this part of Warwickshire (Radley, 2005) so they are probably from the Cotham beds.

Further north, a few insects were reported from Yorkshire. Yorkshire is not very productive for insect specimens of any age, but several were collected from the Late Triassic of Hotham, East Riding (Kelly et al., In press) (SE 868 341). A specimen figured by Tate and Blake (1876) was said to come from the Planorbis Zone based on information from the collector, but they did not record the exact pit where it was found. Sections at "Hotham proper" and "Hotham pit" were detailed by Norwood (1858) who stated that there was no insect limestone present. There are sections of several pits found in the Hotham area (Tate and Blake, 1876), and when insect-bearing horizons were present, they were found below the beds containing *Ostrea* within beds containing *Pleuromya crowcombeia*. This species has been described as characteristic of the lower portion of the *Ostrea* beds (and so the Tilmani Zone) from Yorkshire to Dorset, and *P. tatei* has been described as characteristic of the Langport Member (Richardson and Tutcher, 1916). However, it was also suggested by Richardson and Tutcher (1916) that Tate and Blake (1876) misidentified the Yorkshire *Pleuromya* specimens as *P. crowcombeia* and that they were actually *P. tatei*. If the *Pleuromya* indicated in Tate and Blake (1876) were *P. tatei*, then these insects are likely to be from the Langport Member. The only mention of insects from the Planorbis Zone was by the collector J.W. Kirshaw (Tate and Blake, 1876), but there is no further literature to substantiate this.

2.2.2 Blue Lias Formation

The Blue Lias Formation marks the beginning of a major marine transgression in north west Europe with a shift from the lighter shales and limestones of the Langport Member to darker grey, more organic rich, blocky to laminated, commonly bioturbated mudstones with abundant shells, particularly oysters and mussels (Radley, 2002; Simms, 2004a; Donovan et al., 2005). It is at this level that the distinctive hard, blue limestone known as the *Ostrea* beds or "basement beds" is found. These lower Blue Lias beds also include the "guinea beds" and slightly further up the "firestones", compact, crystalline limestones, abundant in shells and micrite pellets, which generally mark the bottom of the Lias in the Warwickshire area (Woodward, 1893; Richardson, 1912; Old et al., 1991) and are now known as the Stock Green Limestone (Old et al., 1991; Ambrose, 2001; Simms, 2004a) The Grizzle Bed lies above this as a thin bioclastic limestone with shells, vertebrate remains, and echinoid debris. Above this is a series of thick dark grey, laminated mudstones alternating within thinner beds of mostly lighter grey fine-grained, argillaceous limestones where the insects are found. Six limestone beds are reported to have produced insects in the Stratford-upon-Avon area of Warwickshire/ Worcestershire from Osborne's pit, Binton (Brodie, 1845, p. 14; 1886; Tomes, 1878, p. 182; Richardson, 1906) (~SP 138 541), Bidford-on-Avon (Brodie, 1845, 1886; Richardson, 1906, p. 28) (SP 102 527), Wilmcote (Wright, 1860; Brodie, 1861, p. 17; 1868, p. 13; Tomes, 1878) (SP 161 580) and Temple Grafton (Brodie, 1845, p. 74; Tomes, 1878, p. 184) (SP 121 550) in Warwickshire and Nook quarry, Bickmarsh (Brodie, 1845, p. 74) just over the border in Worcestershire (SP 103 501). Some fossils are labelled only as "Stratford-upon-Avon" and may refer to excursions along the railways tracks between Wilmcote and Stratford-upon-Avon (SP 164 580– SP 199 551) during which insects were reported (Brodie, 1888). Two are also labelled as Bishopton Spa (SP 184 563), which is on the outskirts of Stratford-on-Avon on the railways line towards Wilmcote. Most of these sections are composites of different pits in the vicinity of the village of the name so it can be difficult to determine where individual pits were situated (Williams and Whittaker, 1974). Brodie (1845) lists three chief deposits for insects at Bickmarsh and Temple Grafton (C, gravestone bed; D, bottom paving stone; E, white bed) and says that they are also distributed rarely in the upper beds (top rock and thick rock). The limestones were considered by Brodie to correspond exactly in terms of lithology and biological content with the Insect Limestone in Gloucestershire, and indeed the lithology is very similar (Fig. 2.8). This led Brodie to consider them contemporaneous with those in Gloucestershire and Worcestershire, but this is evidently not the case.

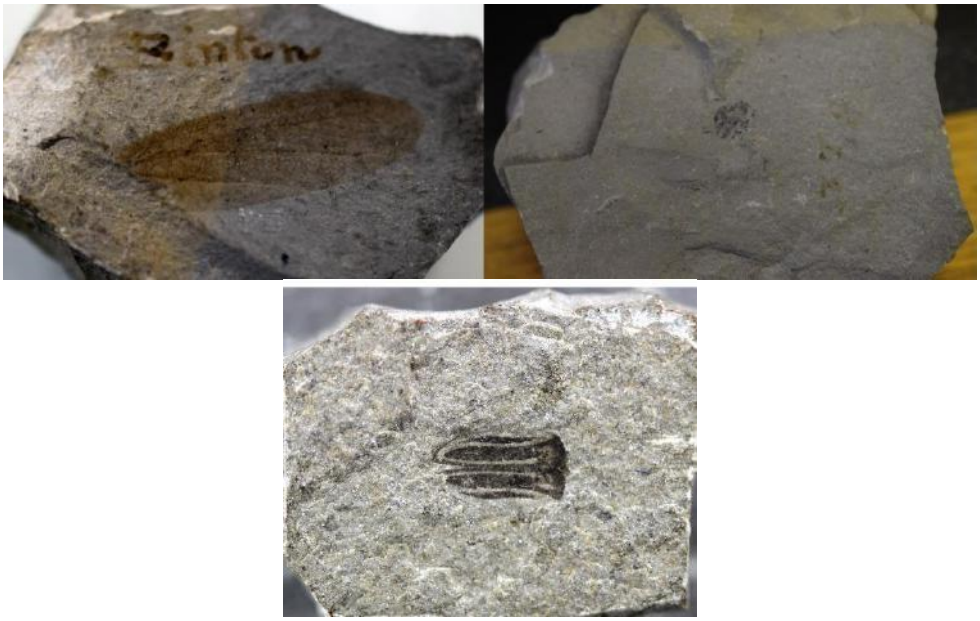

Figure 2.8. Insect-bearing lithology of Binton. Top left: BGS G305; top right: OUMNH J.55101; bottom: NHMUK 6653.

Several of these sections have been discussed recently (Ambrose, 2001; Radley, 2003; Simms, 2004a). At Wilmcote quarry, the base of the Planorbis Subzone was considered to be the grizzle bed and the top was considered to be the "mawms". All of Brodie's limestones are found between these beds and so can be considered to be of Planorbis Subzone age. One insect collected by Tomes was from a higher bed, which is probably in the Johnstoni Subzone of the Planorbis Zone. A further three insects in the collection are labelled from the "firestones". This series is much higher in the succession than the series exposed in Gloucestershire and Worcestershire, appearing above the *Ostrea* beds.

Insects found at Copt Heath (SP 174 779) near Knowle in Birmingham were found *ex situ* as detached pieces in a field but with no section exposed but associated with the "firestones" and "guinea" beds and near limestones containing *Psiloceras planorbis* (Brodie, 1865, 1874, 1887). There is little further information about the exact horizon at which these beds could lie but given the associated beds it is probably from at least near the Planorbis Zone. Barrow-on-Soar in Leicestershire (SK 572 175) exposed similar Lower Lias beds to those at Binton and Wilmcote (Brodie, 1888). A general section was described by Trueman (1918, p. 68), who considered all beds to belong to the Lower Lias, and recent authors still consider these beds to be of Hettangian age (Benson et al., 2012). Two extremely fragmentary specimens of beetle were collected from Cnap Twt quarry in Glamorgan, Wales (Gardiner, 1961) (SS 894 762). The beetle fragments were collected alongside plant material that has been used to estimate the age of the horizons, which were originally thought to be Rhaetian (Gardiner, 1961). Based on further examination of the plant material, the fissures in the St. Brides area, where this quarry is found, have been identified as Hettangian and probably consist of the lower beds of the Wilmcote Limestone Member (Whiteside et al., 2016).

2.2.3 Charmouth Mudstone Formation

The Early Jurassic of the Dorset Coast is very well-studied (Page, 2010) and so insect horizons can be accurately dated. Two of the most prolific localities are Black Ven (SY 357 931) and Stonebarrow (SY 369 930), which produce insects in the same horizons, but which have laterally variable abundance along the coast with the 'flatstones' being more prolific at Stonebarrow and the 'woodstones' more prolific at Black Ven (Ross, 2010). The most prolific insect horizons are found in the Charmouth Mudstone Formation with insects collected from the Turneri Zone: 'Brooki bed' (Bed 74 of Brooki Subzone) and 'Birchi nodules' (Bed 75 of Birchi Subzone); and the Obtusum Zone: 'flatstones', 'woodstones', 'intermediate nodules' and 'yellowstones' (Bed 83 of Obtusum Subzone), 'topstones' (Bed 85 of Stellare Subzone), and 'stellare nodules' (Bed 88 of Stellare Subzone). One insect in the collection is labelled from the alcinoeiforme bed of the Bucklandi Zone (Blue Lias Formation).

When the Charmouth bypass was being constructed, a fossiliferous section of the Charmouth Mudstone Formation was temporarily exposed around the Catherston Lane area of Charmouth (SY 361 935). Insects were collected from the Turneri Zone (Birchi Subzone, Bed 75) and Obtusum Zone (Beds 82, 83h, and 85). Along the coast from the main insect-bearing localities is Monmouth Beach (SY 361 930) where insects have been collected from the Birchi nodules (Birchi Subzone) (Ross, 2010; Kelly et al., 2017). One specimen was recovered from a core drilled approximately 67 km off the south coast of Plymouth in the Western English Channel (Whalley, 1982) (~SY 415 209). The specimen came from the Blue Lias Formation, from the Rotiforme Subzone of the Bucklandi Zone.

One specimen has been collected from the Green Ammonite beds of Golden Cap (SY 406 919) in Dorset by the collector James Carroll. The Green Ammonite beds are formally referred to as the Seatown Marl Member (Page, 2010) which sits at the top of the Charmouth Mudstone Formation within the Lower Pliensbachian (Ainsworth et al., 1998; Cox et al., 1999). The insect was collected from the Figulinum Subzone of the Davoei Zone (James Carroll, pers. comm. 2016).

2.2.4 Whitby Mudstone Formation/Beacon Limestone Formation

There seems to be one horizon in the Lower Toarcian which bears insects, and this runs throughout England. It is in a similar position to other Lower Toarcian insect-bearing horizons that occur throughout a large part of Western and Central Europe (see the descriptions of Germany, Belgium, Luxembourg and the Netherlands below). This horizon is particularly prolific in Germany, but there are also relatively large collections from England, including several well-known historical localities in the Midlands and Somerset and some of the only known fossil insects from Yorkshire.

Dumbleton and Alderton (SP 007 345) in Gloucestershire have been collected from since the 19th century (Brodie, 1845). There are several hills in Gloucestershire from which Toarcian-aged insects have

been collected, and the most prolific are found in the Dumbleton-Alderton area. Dumbleton refers to Dumbleton pit and Alderton refers to Alderton Hill quarry, both of which are on Alderton Hill just south of Dumbleton Hill. This is a well-known locality for insects from the Lower Toarcian fish beds ("Fish and insect beds", "Saurian and fish beds") of the Whitby Mudstone Formation (Simms, 2004b). The fish beds are described as laminated limestone nodules overlying paper shales (Barron et al., 2002) and are contiguous with the fish beds found at Ilminster, as suggested by Williams et al. (2015), being found in the Falciferum Zone.

Additional specimens were collected from Cleeve Hill (SO 984 264) and Nottingham Hill (SO 978 273) near Bishop's Cleeve, from Gretton Hill/Stanley Hill (SP 008 304) in Gloucestershire and from Churchdown Hill/Chosen Hill (SO 880 201) in Gloucestershire. Churchdown Hill was reported to expose the same insect-bearing beds as at Dumbleton (Brodie, 1845; Simms, 2003). The section at Stanley Hill is often referred to as Gretton, a small village on the north side of the hill west of Winchcombe (Woodward, 1893). The section is detailed in Simms (1990), Woodward (1893) and (Tomes, 1886) as exposing middle and Upper Lias beds from the Pliensbachian to the Toarcian. Tomes (1886) stated that the bottom of the quarry exposes clays which lie atop 'middle Lias marlstones'. lower and middle Lias rocks have been described as lithologically similar (Lomax, 2010), whereas those of Toarcian age have an orange/red tint to them (personal observation based on examination of the collections). The lithology of the rocks from Stanley Hill matches that of the rocks from Toarcian horizons, and so the insect horizon is probably Toarcian. This locality may also be called Gretton Hill (Wright, 1878).

Another relatively prolific site for Lower Toarcian insects is the Strawberry Bank *Lagerstätte* from Ilminster (ST 358 148) in Somerset (Moore, 1853). A range of taxa have been collected from Strawberry Bank, including well-preserved vertebrates, but unfortunately the insects are not so well preserved and are of a similar preservation to the other Upper Liassic insects from Gloucestershire. The beds are found in the Beacon Limestone Formation which is split into the lower Marlstone Member and the upper Barrington Member (Williams et al., 2015). The insect horizon is in the Falciferum Zone, similar to the other Toarcian localities.

Three other localities have produced a single insect each, Tilton-on-the-Hill (SK 741 056) in Leicestershire and Skelton (SE 533 600) and Rosedale Wyke (near Whitby) (NZ 878 120) in Yorkshire. There are only two insect specimens from the Lias of Yorkshire, one from Rosedale Wyke held in the private collections of Jörg Ansorge in Germany and the other an isolated beetle elytron (Kelly et al., In press). At Rosedale Wyke, the lowest exposed rocks are of the 'Grey Shale Series' (Howarth, 1962, 1973), now known as the Grey Shale Member of the Whitby Mudstone Formation in the Tenuicostatum Zone (Benton and Taylor, 1984), and the rest of the cliff is the Jet Rock division of the Jet Rock Series (Falciferum Zone, Benton and Taylor, 1984). The specimen is preserved in

pyritized shale and is heavily pyritized itself. According to Benton and Taylor (1984) the Jet Rock shales are abundant in pyrite and fossils are often pyritized. The Bituminous Shales overlie the Jet Rock Shales, and they still contain bands of pyrite, but less so, and the shales are less laminated. This suggests that the insect may have been collected from the Jet Rock Shales and so from the Exaratum Subzone but is at least from the Falciferum Zone.

The specimen from Skelton was collected from Park Pit, an ironstone mine which was described as bearing rocks from the '*annulatus* shales' (Tate and Blake, 1876). The identification of *Ammonites annulatus* was corrected to *A. tenuicostatus* by Buckman (1910), meaning that this horizon is from the Tenuicostatum Zone of the Toarcian and is not coeval with the other Toarcian horizons from the UK. One unidentified specimen was collected from Tilton-on-the Hill, which is a well-documented locality exposing the middle Pliensbachian to Lower Toarcian Whitby Mudstone Formation (Lord, 1982). One insect was reported from the same bed at Spittlegate in Lincolnshire (Morris, 1853), but there are no Lias insects in known collections from Lincolnshire.

2.3 Conclusions

There are three distinct series of insect-bearing limestones in the British Triassic/Jurassic: Lilstock Formation, Blue Lias Formation, and Charmouth Mudstone Formation. There are an additional two beds in the lower Rhaetian for which there are no fossils in the known collections, one bed in the Lower Pliensbachian with only three fossils known, and one in the Lower Toarcian. Several horizons within each series have produced insects, but they tend to concentrate in particular horizons: Lilstock: Insect Limestone/*Pseudomonotis* Bed; Blue Lias: bed 12; Charmouth Mudstone: Brooki bed or woodstones/flatstones. All Lilstock insects are from the upper Rhaetian, zone SAB2; the Blue Lias insects from the Planorbis Zone of the Lower Hettangian, and the Sinemurian insects are more distributed, being found in both the Lower and Upper Sinemurian.

Part 2. Stratigraphy of non-British insect-bearing horizons

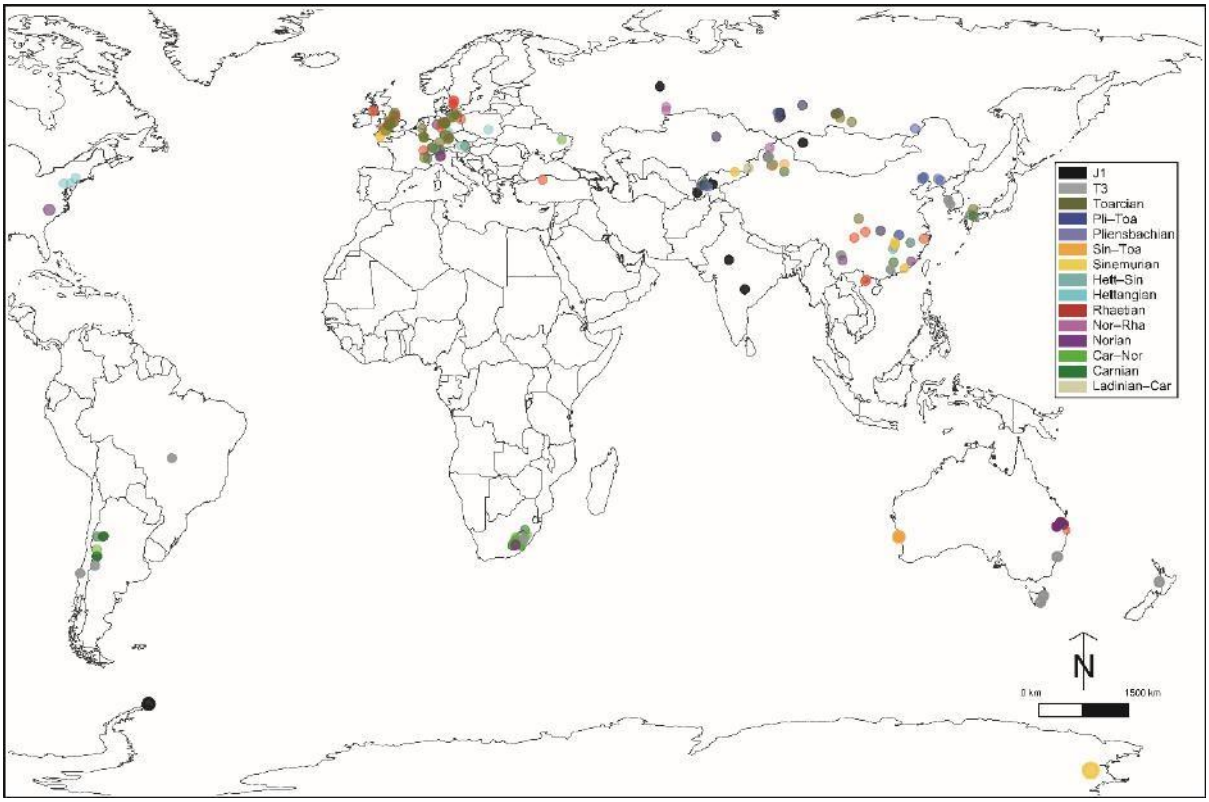

Figure 2.9. Map of all known insect-bearing localities from the Late Triassic to Early Jurassic of the world. Detailed maps for each country/region with specific locality details are provided in the relevant sections below.

Late Triassic and Early Jurassic insects are known from 32 countries and Antarctica (Fig. 2.9) and 89 geological formations (Table 2.1). A comprehensive review of the available literature was carried out to determine the ages of insect-bearing horizons globally. It is important to determine precise ages for fossiliferous horizons so that they can be correlated with other similar horizons around the world. When analysing the fossil record for changes in diversity through time it is vital to know where horizons sit with respect to one another, even if the absolute age is not known.

Table 2.1: Late Triassic–Early Jurassic insect-bearing formations of the world.

Country/Region	Formation	Insect-bearing horizon
Antarctica	Mawson Fm.	Sinemurian
Antarctica	Mount Flora Fm.	Lower Jurassic
Argentina	Los Rastros Fm.	Upper Carnian
Argentina	Potrerillos Fm.	Ladinian/Carnian
Argentina	Cacheuta Fm.	Carnian
Argentina	Llantenes Fm.	Middle–Late Triassic
Australia	Aberdare Fm.	Rhaetian
Australia	Blackstone Fm.	Upper Norian
Australia	Cattamarra Coal Measures Fm.	Sinemurian–Toarcian
Australia	Mount Crosby Fm.	Lower Norian
Australia	Tivoli Fm.	Norian
Australia	Wianamatta Shales	UpperTriassic–Lower Jurassic
Australia	Mount Nicholas Coal Measures	Upper Triassic
Australia	New Town Coal Measures	Upper Triassic
Austria	Lunz Fm.	Lower Carnian
Austria	Gresten Fm.	Lower Hettangian
Belgium	Posidonia Shale Fm.	Lower Toarcian
Brazil	Caturrita Fm.	Middle–Upper Triassic
Chile	Santa Juana Fm.	Middle–Upper Triassic
China	Badaowan Fm.	Lower Sinemurian
China	Baijiantan Fm.	Carnian
China	Beipiao Fm.	Pliensbachian–Toarcian
China	Changliangzi Fm.	Pliensbachian–Toarcian
China	Ganhaizi Fm.	Norian
China	Guanyintan Fm. (Fengjiachong M.)	Pliensbachian–Aalenian
China	Guanyintan Fm. (Paijiachong M.)	Hettangian
China	Hongweikeng Fm. (Shezhu M.)	Carnian
China	Huangshanjie Fm.	Upper Carnian
China	Jinji Fm. (upper M.)	Sinemurian
China	Menkoushan Fm.	Hettangian–Sinemurian
China	Nalaqing Fm.	Upper Triassic
China	Sangonghe Fm.	Sinemurian–Toarcian
China	Sanqiutian Fm.	Norian–Rhaetian
China	Lufeng Fm.	Hettangian
China	Wenbinshan Fm.	Upper Norian
China	Wuchang Fm.	Pliensbachian–Toarcian
China	Wuzao Fm.	Rhaetian
China	Xiahuayuan Fm.	Pliensbachian–Toarcian
China	Xiaoping Fm.	Upper Triassic
China	Xujiahe Fm.	Rhaetian
China	Zaoshang Fm.	Sinemurian
China	Zijiachong Fm.	Late Triassic
France	unknown	Rhaetian
France	Keuper Fm.	Carnian
Germany	Arnstadt Fm.	Norian
Germany	Bayreuth Fm.	Lower Hettangian
Germany	Exter Fm.	lower Rhaetian
Germany	Hassberge Fm.	Upper Carnian
Germany	Posidonia Shale Fm.	Lower Toarcian

India	Kota Fm.	Pliensbachian–Toarcian
Italy	Argilliti di Riva di Solto Fm.	Upper Norian
Japan	Momonoki Fm.	Middle Carnian
Japan	Nishinakayama Fm.	Lower Toarcian
Kazakhstan	Dubovskaya Fm.	Pliensbachian
Kazakhstan	Koldzat Fm.	Ladinian–Carnian
Kazakhstan	Kushmurun Fm.	Lower Jurassic
Kazakhstan	Tologoi Fm.	Norian–Rhaetian
Kyrgyzstan	Dzhil Fm.	Sinemurian
Kyrgyzstan	Madygen Fm.	Carnian
Kyrgyzstan	Sagul Fm.	Toarcian–Middle Jurassic
Liechtenstein	Keuper Fm.	Carnian
Luxembourg	Posidonia Shale Fm.	Lower Toarcian
Mongolia	Zhargalant Fm.	Toarcian
Netherlands	Posidonia Shale Fm.	Lower Toarcian
New Zealand	unknown	Upper Triassic
Poland	Zagaje Fm.	Lower Hettangian
Russian Federation	Abasheva Fm.	Pliensbachian
Russian Federation	Cheremkhovo Fm.	Toarcian
Russian Federation	Korkino Fm.	Upper Triassic
Russian Federation	Makarova Fm.	Pliensbachian
Russian Federation	Osinovo Fm.	Pliensbachian
S. Africa/Lesotho	Molteno Fm.	Carnian, Norian, or Carnian/Norian
South Africa	Cave Sandstone	Carnian–Norian
South Korea	Amisan Fm.	Late Triassic
Sweden	Höganäs Fm.	lower Rhaetian
Switzerland	Staffeleg Fm.	Middle Hettangian
Switzerland	Posidonia Shale Fm.	Lower Toarcian
Tajikistan	Kugitang Fm.	Early Jurassic
Tajikistan	Sulyukta Fm.	Pliensbachian
Turkey	Çakrazboz Fm.	Rhaetian
Ukraine	Protopivka Fm.	Carnian
UK	Beacon Limestone Fm.	Lower Toarcian
UK	Blue Lias Fm.	Lower Hettangian
UK	Charmouth Mudstone Fm. (Turneri)	Lower Sinemurian
UK	Charmouth Mudstone Fm. (Obtusum)	Upper Sinemurian
UK	Charmouth Mudstone Fm. (Davoei)	Lower Pliensbachian
UK	Lilstock Fm.	upper Rhaetian
UK	Westbury Fm.	lower Rhaetian
UK	Whitby Mudstone Fm.	Lower Toarcian
US	Cow Branch Fm.	Lower Norian
US	Mount Toby Fm.	Hettangian
US	Shuttle Meadow Fm.	Hettangian
US	Towaco Fm.	Hettangian
Vietnam	unknown	Rhaetian

2.4 WESTERN LAURASIA

Austria.—Late Triassic insects have been collected from the Lunz Formation (Meller et al., 2011), which is suggested to be early Carnian (Hornung, 2010). Insect eggs have also been found in amber from the same locality (Pott et al., 2008; Fischer et al., 2017). Two species were mentioned from the 'Lias of Pechgraben' by Heer (1865, p. 91–92, footnotes), but little further information was given. The Gresten Formation is found in the lower beds of the Gresten Klippen Zone which are intercalated with coal and is dated as Hettangian (Ślączka et al., 2009). This locality should not be confused with the locality of Pechgraben in Germany, discussed below.

France.—A single specimen was described from the Late Triassic of France (Meunier, 1907; Nel et al., 2001) and is referred to the Rhaetian. There is no further information in the literature regarding the stratigraphy of this locality, so it is difficult to confirm this age but the horizon from which the insects were collected is still considered to be Rhaetian (andré Nel pers. comm. June 2017). France is better known for its Middle Triassic insects from the Gres a Voltzia Formation (Aristov et al., 2011).

Germany.—Many Triassic/Jurassic insects have been collected from Germany (Fig. 2.10), particularly the well-known Lower Toarcian beds which have produced hundreds of insect species from Grimmen (Zessin, 1983a, 1987; Ansorge, 1996), Bavaria (Kuhn, 1952; Vršanský and Ansorge, 2007), lower Saxony (Bode, 1953; Ansorge, 2002), and Mecklenburg-Vorpommern (Handlirsch, 1906; Zeuner, 1939). Many are from the Posidonia Shale Formation (Fig. 2.11), and most are found in the Falciferum Zone: Exoratum Subzone (Ansorge, 2003) and are therefore contemporaneous with those from the Severn Valley, Somerset, and Yorkshire. Those from the productive locality of Dobbertin are from the "Green Series" of similar stratigraphic position to those form the Posidonia Shale Formation (Ansorge, 2003). This horizon is wide-ranging and is also found in Switzerland, Belgium, Luxembourg, and the Netherlands (Nel et al., 1993; Henrotay et al., 1998; Fleck et al., 2003). Middle to Upper Norian insects are known from the Arnstadt Formation of Vlotho-Bonneberg (Zeuner, 1930) and the "insect bed" of Langenberg, Lower Saxony, which is the richest Late Triassic fauna of Germany (Prokin et al., 2013). The Arnstadt Formation spans the middle to Upper Norian (Bachmann and Kozur, 2004). The "insect bed" of Langenberg is found within beds with a high diversity of the Norian conchostracan *Shipingia gerbachmanni* (Hauschke and Kozur, 2011), indicating the Upper Norian (Sullivan et al., 2011).

Several Carnian-aged insects were collected from the Schönbachsmühle quarry, near Ebelsbach from the Hassberge Formation (Prokin et al., 2013), which is Upper Carnian (Havlik et al., 2013). The upper Keuper: Exter Formation has produced several insects from Gartz (Barth et al., 2013) and Teufelsgrabens (Handlirsch, 1912). The Exter Formation generally correlates with the Westbury Formation of the UK (Barth et al., 2018), indicating a lower Rhaetian age.

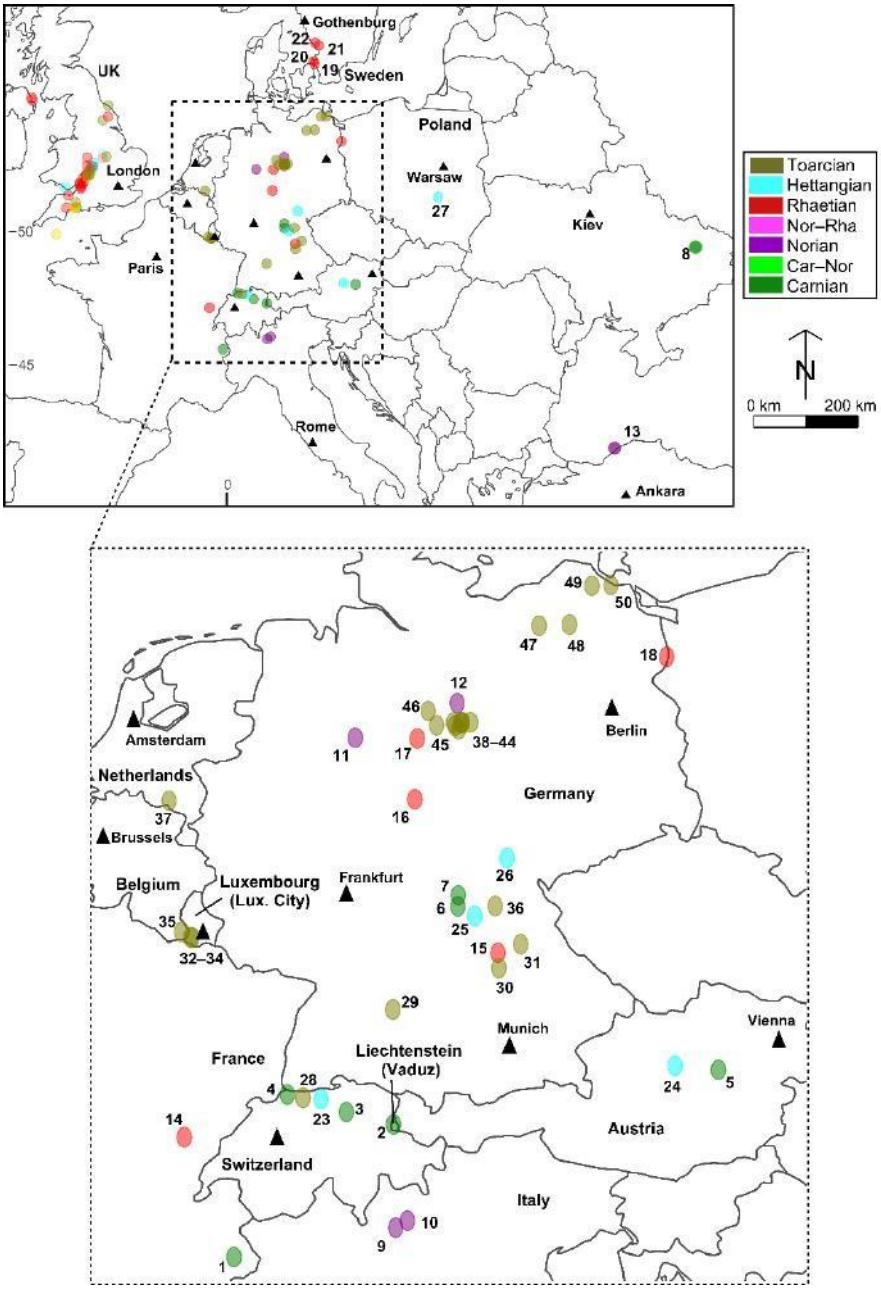

Figure 2.10. Map of all known insect-bearing localities from Europe and Western Asia with detailed map of Central Europe. Non-UK localities are as follows: 1. Dent de Villard, FR; 2. Vaduz, LI; 3. Mythen-Berg, CH; 4. Rutihard, CH; 5. Rudolfstollen waste heap, AT; 6. Eltmann quarry, DE; 7. Schönbachsmühle quarry, DE; 8. Garazhovka, Ukraine; 9. Ponte Giurino, IT; 10. Bergamo, IT; 11. Vlotho-Bonneberg road, DE; 12. Langenberg, DE; 13. Tchakras, Turkey; 14. Fort-Mouchard, FR; 15. Teufelsgrabens, DE; 16. Blatt Witzenhausen, DE; 17. Kralah, DE; 18. Gartz, DE; 19. Kulla Gunnarstorp, SE; 20. Höganäs, SE; 21. Bjuf, SE; 22. North of Sofiero, SE; 23. Schambelen, CH; 24. Pechgraben, AT; 25. Strullendorf, DE; 26. Sandpit Küfner, DE; 27. Odrowaz, PL; 28. Hemmikon, CH; 29. Holzmaden, DE; 30. Kerkhofen, DE; 31. Mistelgau, DE; 32. Sanem, LU; 33. Luxguard quarry, LU; 34. Bascharage, LU; 35. Belgium; 36. Feuermühlenberg, DE; 37. Netherlands; 38. Schandelah, DE; 39. Hondelage, DE; 40. Sehlde & Ringelheim, DE; 41. Beienrode, DE; 42. Grassel, DE; 43. Flechtorf, DE; 44. Volkmarsdorf, DE; 45. Hattorf, DE; 46. Schlewecke am Harz, DE; 47. Schwinzer brickyard, DE; 48. Dobbertin, DE; 49. Lehmhagen, DE; 50. Schönenwald, DE.

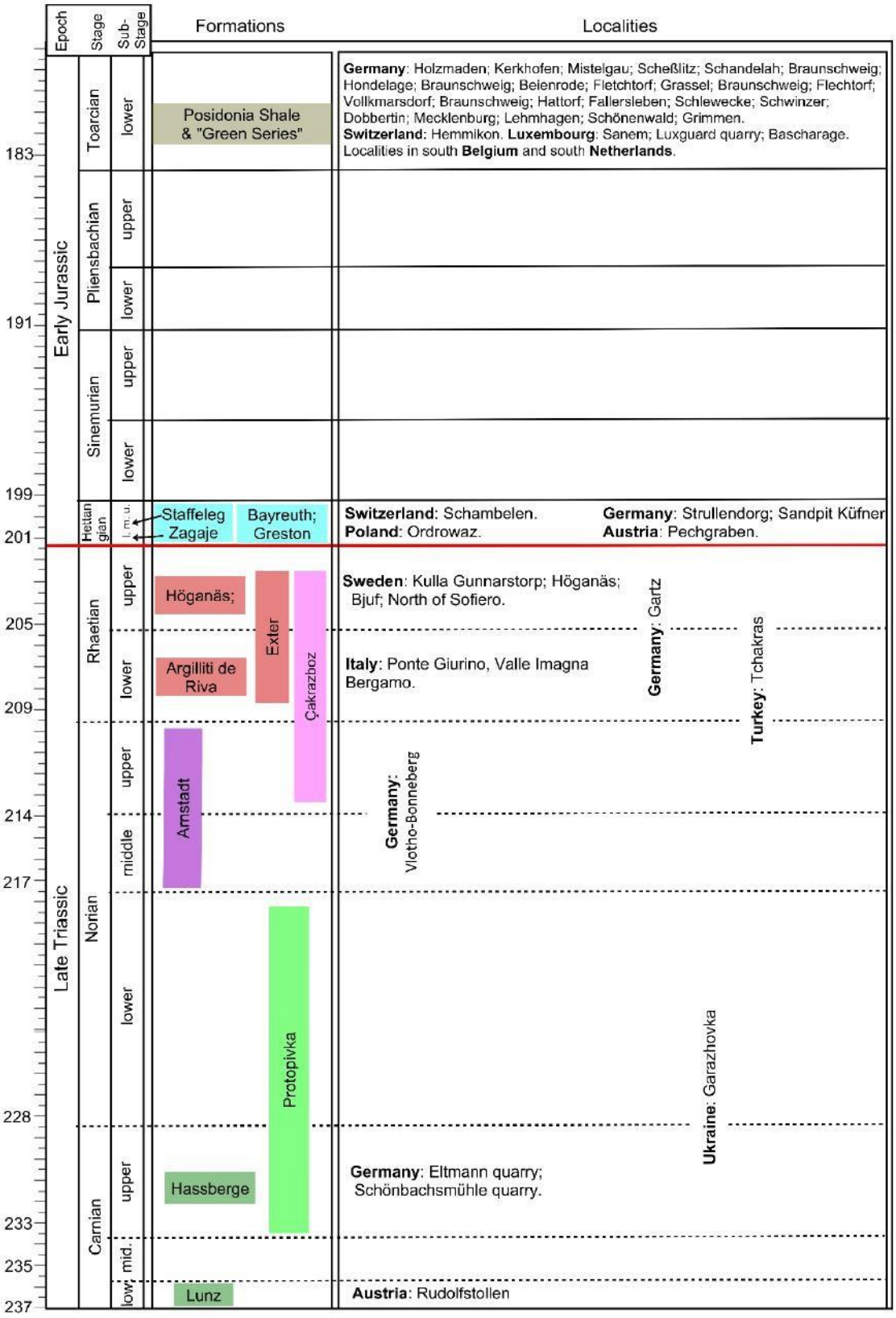

Figure 2.11. Stratigraphic chart of European insect-bearing formations and localities.

Italy.—A few insects have been found in the Late Triassic Argilliti di Riva di Solto Formation near Bergamo (Whalley, 1986) and Ponte Giurino, Valle Imagna (Wild, 1994). The insects from Bergamo were collected from organic shales attributed to the lower Rhaetian and those from Ponte Giurino from the Upper Norian. However, insects are only found in the lower black marl beds of this formation according to Renesto (2008), and so it is likely that the insects described by Whalley (1986) are also of Upper Norian age.

Liechtenstein.—A couple of Late Triassic insects were collected from the Keuper rocks of Mythen-Berg (Heer, 1877), and Vaduz in Liechtenstein (Heer, 1853). They were described as probably being Carnian based on floral content, but there is little information on the exact level of the insect-bearing horizons and so they could lie anywhere between the upper Ladinian to Norian.

Poland.—An insect-bearing horizon was found in a section at Odrowaz, Swietokrzyskie (Popov, 1996). The section was assigned to the Zagaje Formation (Pieńkowski and Gierliński, 1987) which overlies Rhaetian sediments. The insect-bearing horizon is found in the lower part of the formation and is dominated by dark-grey and olive-green mudstones and siltstones interbedded with coal layers and preserving plant fossils (Wegierek and Zherikin, 1997). Insects were collected from a layer of grey to yellowish-grey sandy mudstone with sparse plant remains (mostly shoots of the conifer genus *Hirmeriella*). The Zagaje Formation in the region of this locality sits entirely in the lower Planorbis Zone (Wegierek and Zherikhin, 1997). Although (Niedźwiedzki and Pieńkowski, 2016) consider that in certain areas of the Holy Cross Mountain region the formation spans into the Rhaetian below, it does not in the region from which the insects were collected. It is therefore likely that the insects are of a similar age to those of the English fauna.

Sweden.—Insects were collected from the Höganäs Formation of Sweden by Heer (1878) and are also listed in Scudder (1891). Based on a survey of the collection at the Swedish Royal Museum of Natural History this assemblage is much more diverse than previously thought and so is worthy of further investigation. The formation is considered Rhaetian to Hettangian in age (Ahlberg et al., 2003; Vajda et al., 2013) and insects were collected from black coal slate or fine-grained grey limestone (Heer, 1878, p. 193) alongside plant material. This could be a reference to the carbonaceous shales of the Rhaetian Bjuv Member as described by Pott and McLoughlin (2009) which is considered lower Rhaetian, contemporaneous with the upper beds of the Westbury Formation (Barth et al., 2018). This member directly underlies the Hettangian Helsingborg Member and so is probably upper Rhaetian. This means that insects from here are likely to be coeval with those found in the Langport Member of south-west England and the *Pseudomonotis* beds of the English Midlands.

Switzerland.—The ‘Insektenmergel’ (now the Schambelen Member of the Staffeleg Formation), of Switzerland was a particularly prolific horizon for insects described by Heer (1852) and summarised by Goss (1879). The lithology and fossil content of the section at Schambelen was described in detail by Heer (1865, p. 62–64). Early Jurassic ammonite genera (*Psiloceras* and *Schlotheimia*) were recorded in beds below the insect-bearing horizons (primarily bed 11 but also rarely from beds 7 and 9) so we can be confident that they are not Triassic. Bed 11 lies 2.9 m (“9.5 feet”) above the boundary with the Keuper. In other areas, erosion at the base of the Schambelen Member has led to the member directly overlying Norian rocks (Reisdorf et al., 2011). The member has previously been considered to be from the Planorbis Zone (Maisch et al., 2008). It is more recently considered to lie within the Liassicus Zone based on the lithology of the whole area of the Schambelen Member, with its lower beds possibly synchronous with the Planorbis Zone (Reisdorf et al., 2011). Bed 11 lies around the middle of the section and so even if the lower beds span into a different zone it is likely that the main insect-bearing horizon is still considered to lie in the Liassicus Zone. Two species have been described from the Keuper rocks of Switzerland (Heer, 1853) but the horizon is unclear.

Turkey.—A private collection of insects belonging to Charles Florent was described from the Çakrazboz Formation of Tchakras, Amasra region, Turkey by Laurentiaux (1946), who considered them to be Rhaetian based on the presence of ‘*Estheria minuta*’. This species is characteristic of the Rhaetian beds of England, with historical accounts describing the Estheria beds as lower Rhaetian. However, it is also known from throughout the Late Triassic and perhaps into the Middle Triassic (Kozur and Weems, 2010). The flora of the formation has been described as latest Triassic (Alişan and Derman, 1995) and so it is possible that the insect horizon is Norian to Rhaetian.

Ukraine.—A few insects were collected from the Protopivka Formation of Garazhovka, Kharkiv, Ukraine, which is only indicated as Late Triassic (Aristov, 2005). Recently authors have suggested an Upper Carnian age (Shcherbakov, 2008a), but there is little literature regarding the insect-bearing horizons of this formation. It is herein considered Carnian.

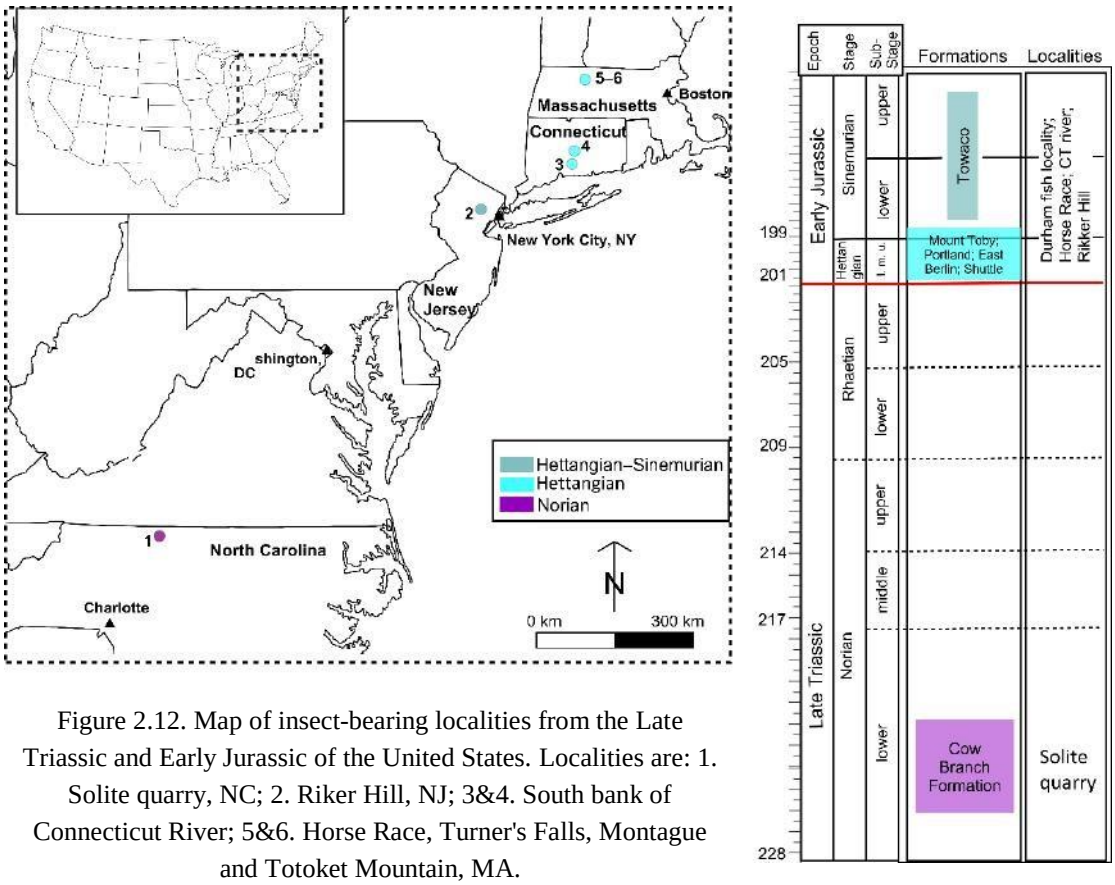

Figure 2.12. Map of insect-bearing localities from the Late Triassic and Early Jurassic of the United States. Localities are: 1. Solite quarry, NC; 2. Riker Hill, NJ; 3&4. South bank of Connecticut River; 5&6. Horse Race, Turner's Falls, Montague and Totoket Mountain, MA.

United States of America.—There is a large collection of insects from the Cow Branch Formation of the Solite quarry on the Virginia/North Carolina border (Fig. 2.12). This insect bearing horizon was originally thought to be Carnian in age, but the formation is now considered to cross the Carnian/Norian boundary (Muttoni et al., 2004; Heckert et al., 2012), meaning that the insect-bearing horizon, which is in the upper layers, is probably Lower Norian. Several localities further north of the East Coast of the United States have borne insects from the Early Jurassic of the Newark Supergroup. The Hettangian Member A of the Mount Toby Formation of Horse Race (Montague and Gill), Massachusetts; lower–middle Portland Formation of Connecticut (Hitchcock, 1858; Huber et al., 2003); Shuttle Meadow Formation of the Durham fish locality, Durham, Connecticut (Huber et al., 2003); and the East Berlin Formation of Cromwell, Connecticut. Also, the Towaco Formation of Riker Hill quarry, New Jersey (Olsen, 1995), which is considered Hettangian–Sinemurian.

2.5 CENTRAL AND EASTERN LAURASIA

2.5.1 East Asia

China.—The majority of Chinese Late Triassic to Early Jurassic insects are collected from the Junggar Basin of Xinjiang Province in North-western China but other horizons are found distributed through much of the country (Figs 2.13, 2.14). Late Triassic insects have been collected from the Baijiantan Formation in the northwest of the basin, the Huangshanjie Formation in the south of the basin and the Karamay Formation in the south and the northwest of the basin (Ashraf et al., 2010). The Karamay Formation was considered entirely Middle Triassic (Bian et al., 2010; Sun et al., 2010; Choulet et al., 2013) until Late Triassic plant fossils were found in the upper parts of the formation (Shi et al., 2015). Fossils belonging to the *Danaeopsis-Symopteris* (=*Danaeopsis-Bernoullia*) flora were described, moving the upper boundary of the formation into the Upper Triassic, and probably closer to the Middle Carnian. The Karamay Formation is unconformably overlain by the Baijiantan Formation in the northwest of the Junggar Basin and by the Huangshanjie Formation in the south of the basin, both of which have produced insects (Ashraf et al., 2010; Zheng et al., 2017).

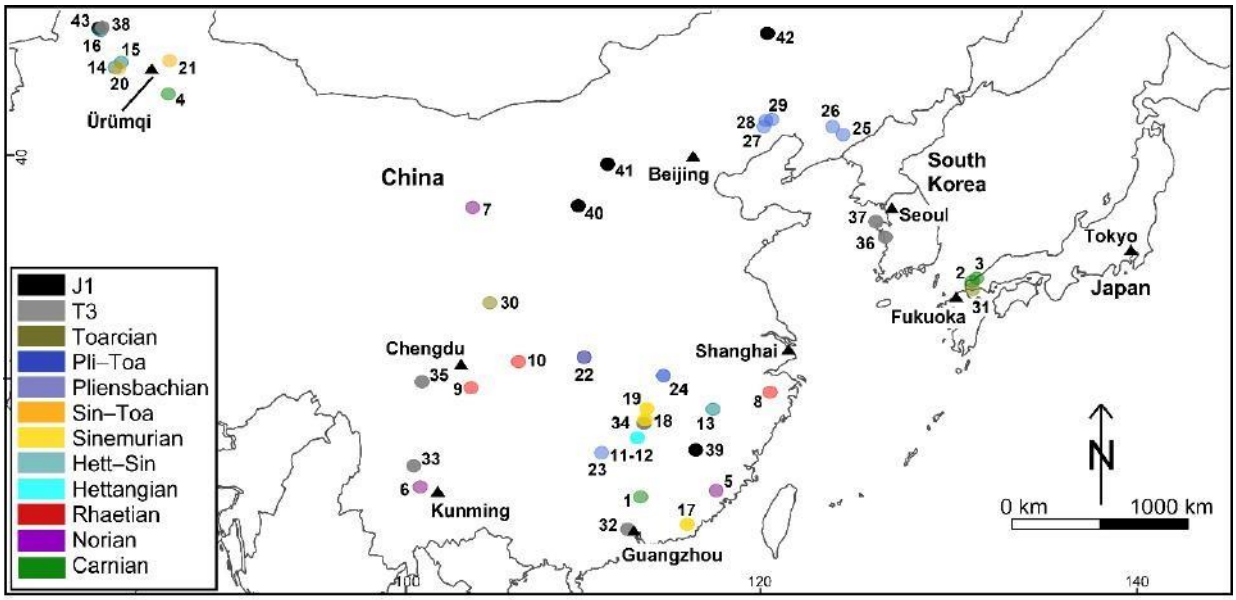

Figure 2.13: Map of Late Triassic to Early Jurassic insect-bearing localities of East Asia (excluding Mongolia). All localities are China unless otherwise stated: 1. Niugudun; 2. Okubata, 3. Japan; Hazegatani coal mine, Japan; 4. Kerjie; 5. Xialiao; 6. Lufeng County; 7. Wuzao village; 8. Chuanshandong; 9. Hongqi coal mine; 10. Meitian; 11. Yuanzhu;; 12. Meixi; 13. Shichang; 14. Nan'anchihai; 15. Tuzigou; 16. Huizhai; 17. Chengtanjiang; 18. Shijiaba; 19. Honggou; 20. Xidagou; 21, Shazhenxi; 22. Jinshandian; 23. Dapianling; 24. Benxi; 25. Yangshugou; 26. Mayingzi; 27. Kuntouyingzi; 28. Huajiaozi; 29. Toyora, Japan; 30. Benggang; 31. Yongren County; 32. Chengtanjiang; 33. Myungcheon-dong, South Korea; 34. Jeongeon Area, South Korea; 35. Shendigou outcrop; 36. Karamay City.

The Baijiantan Formation is considered to be Late Triassic based on megaspore assemblages and comparisons with the Haojiagou and Huangshanjie formations in the south of the basin (Luo et al., 2007; Zheng et al., 2017). Only Late Triassic spore assemblages have been found in the Baijiantan Formation, so it is likely that its upper boundary is at or below the TJB. The Huangshanjie Formation is considered to be Upper Carnian, underlying the Haojiagou Formation which rests on the Carnian/Norian boundary (Zheng et al., 2017). Again, no Early Jurassic faunas or floras have been found in the Haojiagou Formation, indicating that its upper boundary lies similarly to the Baijiantan Formation. A palynological analysis of the southern Junggar Basin provided evidence for the Late Triassic age of the Haojiagou Formation (Sha et al., 2011), possibly Norian–Rhaetian (Sun et al., 2010; Sha et al., 2015; Zheng et al., 2017).

Most Early Jurassic insects from China have been collected from the Badaowan Formation (Yan and Zhang, 2010; Zheng et al., 2017) of the Junggar Basin in which there is also a later Early Jurassic horizon found in the Sangonghe Formation (Zhang et al., 2003). The Badaowan formation is understood to be Early Jurassic in age, probably spanning the Hettangian and at least into the Sinemurian (Ashraf et al., 2010; Sha et al., 2011, 2015; Zheng et al., 2017), indicating that insect horizons found in the lower part of the formation are probably Hettangian and those in the upper part are probably Sinemurian. The Sangonghe Formation lies above the Badaowan Formation and is considered to be upper Lower Jurassic (Ashraf et al., 2010), lying within or around the Toarcian, but may also extend in to the Upper Sinemurian (Sha et al., 2011).

Late Triassic insects are found in several formation around the country (Lin, 1986; Wang and Smith, 1986). The age of the Hongweikeng Formation is constrained between 235 Ma and 229 Ma (Pang et al., 2014) which places the formation at the middle to Upper Carnian. At least parts of the Jinji Formation are Sinemurian based on ammonite content. The Ganhaizi Formation of Yunnan Province (Lin, 1977) is part of the Yipinglang Group, which is considered to be entirely Norian according to (Fang et al., 2000). The Wuzao Formation of Zhejiang Province (Lin, 1980) is described as uppermost Triassic. Insects from the Zijiachong (=Tzuchiachung), Guanyintan and Zaoshang (=Shikang) formations of Hunan Province were reported in Lin (1986) as Early Jurassic. The Zijiachong Formation is recorded in the Jurassic of the Jiangxi Province (neighbouring Zhejiang) by Zhang (2010) but is recorded in other sources as Triassic, from Zhejiang Province (Teng et al., 2010). The Menkoushan Formation of Fuijan Province was recorded in Huang et al. (1991) and is considered to be Early Jurassic age (Tan et al., 2006), the insects are found in the lower part of the formation according to (Huang et al., 1991).

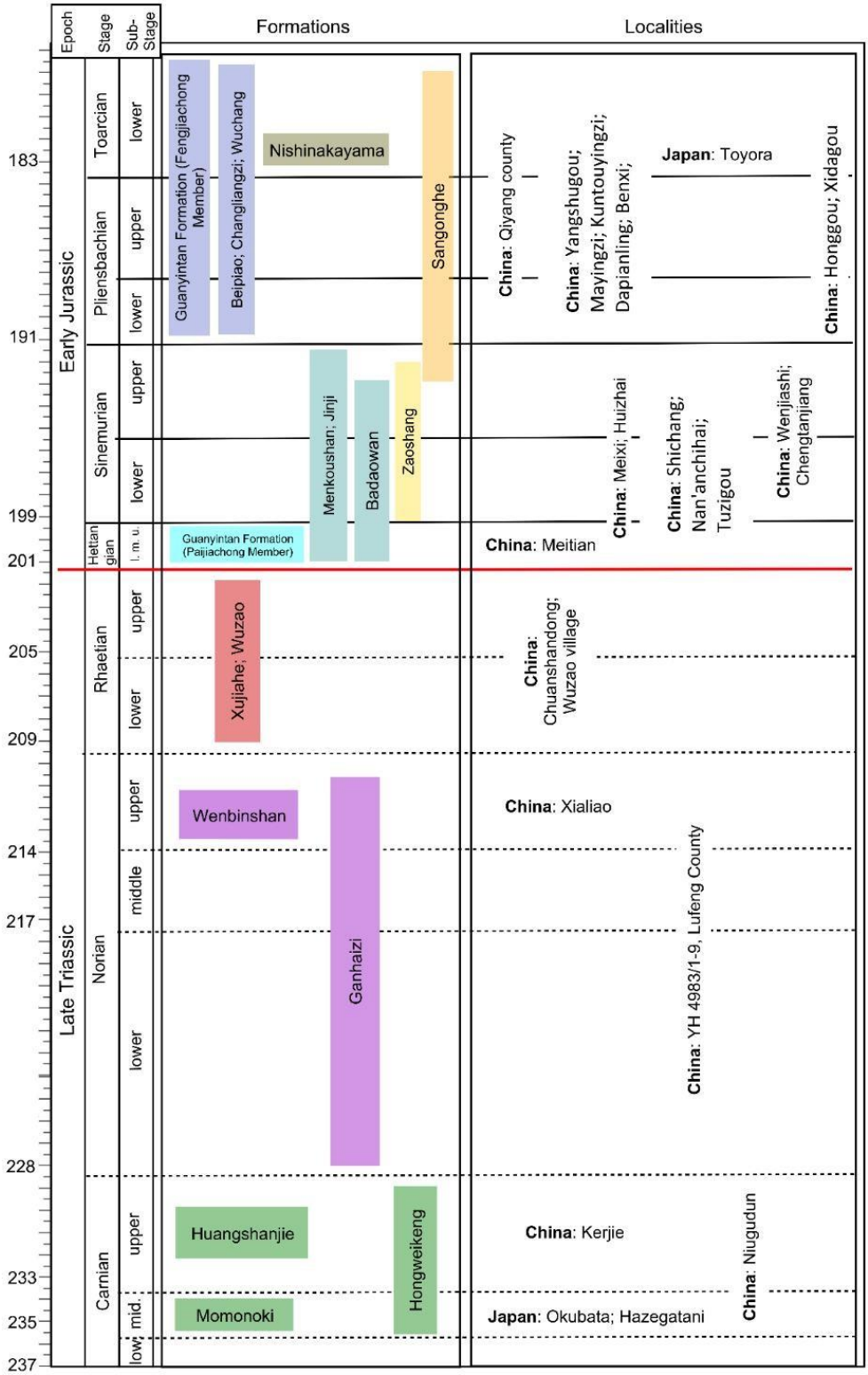

Figure 2.14. Stratigraphic chart of East Asian insect-bearing formations and localities.

Japan.—There are several horizons known from Japan with a few specimens each. Several insects were collected from coal layers of the Momonoki Formation of Omine, Japan (Fujiyama, 1973, 1991). Based on the fossil flora and fauna, the age of the formation is estimated as Middle Carnian (Katayama, 1938). Other Triassic aged insects were collected from the Iwamuro Formation, which was described as Early Jurassic based on a plant fossil assemblage similar to other *Danaeopsis-Bernoullia* assemblages (Kamikubo and Takeuchi, 2011). However, the *Danaeopsis-Symopteris* (= *Danaeopsis-Bernoullia*) flora is usually considered Late Triassic (Sha et al., 2015) and so these insects were probably deposited in the Late Triassic. Early Jurassic insects are known from the Nipponicum Zone (Toyora Group: Nishinakayama Formation) of Toyoro (Fujiyama, 1974). The Nipponicum Zone has been correlated with international ammonite zones (Nakada and Matsuoka, 2011), corresponding to the upper half of the Paltus Zone and most of the Helianthoides Zone of the Lower Toarcian.

South Korea.—The Amisan Formation of South Korea has also produced Triassic-aged insects but, although the associated plants have been well studied, the insects still require identification and taxonomic work (Nam and Kim, 2014). The age of the formation is contentious; biostratigraphically it is dated as Late Triassic based on floral and conchostracan assemblages (Kimura and Kim, 1984). Further floral evidence was put forward by Kim (2001) who identified several new plant species comparable with those described from the Late Triassic of China and Japan. Comparisons are also made with species from Central Asia and eastern Ukraine and although similar, differences are noted.

K-Ar dating of illites from argillaceous shales of the Amisan Formation gave ages of ~157 Ma and ~140 Ma for authigenic illitization of these shales (Egawa and Lee, 2011), suggesting a Middle Jurassic age. However, there are issues with this dating technique and some authors have suggested that the results are often much younger than they should be (Perry, 1974; Clauer et al., 1997). Subsequent authors have not agreed with this Middle Jurassic age estimation and retain use of the Late Triassic age (e.g. Nam and Kim, 2014).

2.5.2 Northern and Central Asia

There is a long history of collecting Mesozoic insects from regions in Central and Northern Asia by Russian palaeoentomologists. The majority are from Kyrgyzstan, with other large collections from Tajikistan, Kazakhstan, and Siberian Russia (Fig. 2.15), no known localities exist in European Russia. The collections of Late Triassic–Early Jurassic insects held at the Paleontological Institute of the Russian Academy of Sciences (PIN) are by far the largest in the world, e.g. 20,000 recorded from the Madygen Formation of Kyrgyzstan, Shcherbakov (2008b); 3800 from the Dzhil Formation of Kyrgyzstan, Khramov and Makarkin (2015). There have been many important monographs and smaller publications discussing and describing this vast diversity (e.g. Martynov, 1925a, 1925b, 1925c; Martynova, 1943; Sharov, 1968; Ponomarenko, 1985; Rasnitsyn, 1985; Sinitshenkova, 1987;

Shcherbakov, 2008b; Khramov and Makarkin, 2015) leading to the description of at least 800 species from the Late Triassic and Early Jurassic according to the PBDB.

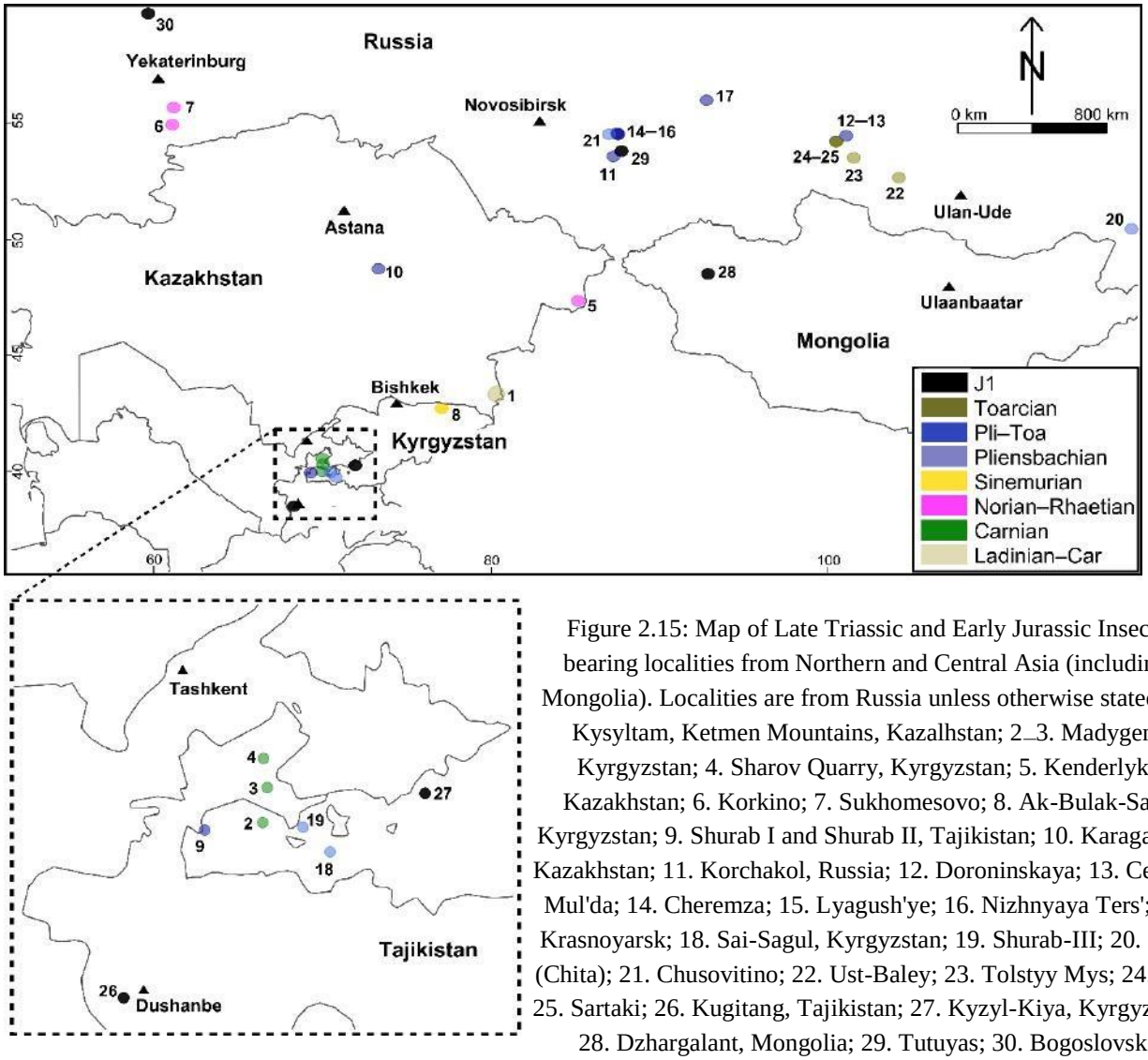

Figure 2.15: Map of Late Triassic and Early Jurassic Insect-bearing localities from Northern and Central Asia (including Mongolia). Localities are from Russia unless otherwise stated: 1. Kysyltam, Ketmen Mountains, Kazalhstan; 2–3. Madygen, Kyrgyzstan; 4. Sharov Quarry, Kyrgyzstan; 5. Kenderlyk, Kazakhstan; 6. Korkino; 7. Sukhomesovo; 8. Ak-Bulak-Say, Kyrgyzstan; 9. Shurab I and Shurab II, Tajikistan; 10. Karaganda, Kazakhstan; 11. Korchakol, Russia; 12. Doroninskaya; 13. Central Mul'da; 14. Cheremza; 15. Lyagush'ye; 16. Nizhnyaya Ters'; 17. Krasnoyarsk; 18. Sai-Sagul, Kyrgyzstan; 19. Shurab-III; 20. Zola (Chita); 21. Chusovitino; 22. Ust-Baley; 23. Tolstyy Mys; 24. Iya; 25. Sartaki; 26. Kugitang, Tajikistan; 27. Kyzyl-Kiya, Kyrgyzstan; 28. Dzhargalant, Mongolia; 29. Tutuyas; 30. Bogoslovsk.

Although the diversity of these insect-bearing horizons is vast, there are difficulties with applying a precise age to them as they are generally found in terrestrial or semi-terrestrial deposits which are difficult to correlate with global sections and international stratigraphic frameworks (Fig. 2.16). The stage-level ages listed in the PBDB are probably over ambitious given the evidence available (Alexandr Rasnitsyn pers. comm. June 2016). Most age estimates are based on palaeobotanical analysis and there has been some important work carried out attempting to establish ages for these formations based on micro- and macrofloral assemblages (Kuzichkina et al., 1958; Dobruskina, 1977, 1995; Aliev et al., 1981; Kiritchkova and Doludenko, 1996, 1996; Mogutcheva, 2009, 2014; Panov and Baraboshkin, 2015; Frolov et al., 2017; Kiritchkova et al., 2017). Additionally, there have been

ages suggested for these formations based on the insect assemblages (Ponomarenko, 2002a; Sukacheva and Rasnitsyn, 2004; Shcherbakov, 2008a) but these estimations do not always correspond, so age ranges can be quite broad, covering at least two stages (e.g. Pliensbachian–Toarcian) or epochs (e.g. Early–Middle Jurassic).

Kazakhstan.—Insects were collected from the Koldzat Formation of Kysyltam, Kazakhstan, which is considered Ladinian to Carnian based on megafloral assemblages (Shcherbakov et al., 1995). The Tologoi formation of Kenderlyk, Kazakhstan (Sinitshenkova, 1987; Papier and Nel, 2001) is generally considered to be Late Triassic (Aristov, 2005). It has been suggested to be Norian–Rhaetian (Shcherbakov et al., 1995), which was followed by de Jong et al. (2008), but also Late Carnian–Norian (Shcherbakov, 2008a). However, similar conchostracan assemblages have been described from the Yangcaogou Formation in western Liaoning (Late Triassic, Zhang et al., 2010); the Baitianba Formation of Sichuan Province (Early Jurassic, Meng et al., 2005; Deng et al., 2012) and Wennan Formation of Shandong Province (Early Cretaceous, Yang et al., 2013). But it differs from the *Euestheria* assemblage of the Yanchang Formation (Late Triassic) and the Palaeolimnadiopseoidea assemblage of Fuxian Formation (Early Jurassic) (Shuwen, 1987). It is therefore difficult to estimate the age of this horizon, so we consider it to be Late Triassic age as suggested by previous authors.

Kyrgyzstan.—The Madygen Formation of Madygen, Kyrgyzstan is the most prolific, with over 20,000 insects collected (Kogan et al., 2009). Outcrop 14 (Sharov Quarry) is the main locality for fossil insects from the Madygen Formation and is known as Dzhaylyau-Cho (=Urochishche Dzhaylyaucho) in the northern area (Dobruskina, 1995). Over 80% of Madygen insects were collected from this locality (Voigt et al., 2006, =LII/1). The formation is generally considered as entirely Triassic based on megafloral diversity and is estimated as Middle Triassic: Ladinian to Late Triassic: Carnian (Dobruskina, 1995; Shcherbakov, 2008b). Some authors have suggested a Carnian age based on the entomofauna (Ponomarenko, 2002a), but a Ladinian age has been suggested to be more probable based on the primitive nature of some groups of insects compared to deposits from South Africa and Australia (Shcherbakov, 2008b). Further to this point, Voigt et al. (2017) considered the insect assemblage to be mostly likely late Middle Triassic in age based on it having the second oldest dipteran fauna after Vosges, France (Anisian); earliest known Hymenoptera; and in comparison with the "Carnian" assemblages of Australia and South Africa. Also, based on branchiopods only known from the late middle and Late Triassic. However, as discussed in section 2.5 below, many of the horizons from Gondwana previously considered Carnian are now considered Norian, and so a Carnian age may be likely for the Madygen insects. Especially for those insects found in the upper Member (Béthoux et al., 2010), which lies directly below "Jurassic and Cretaceous" rocks (Dobruskina, 1995).

Furthermore, the Noenian Formation of Mongolia correlates with the Madygen Formation and is considered Carnian based on the brachiopod Kazacharthra (Ponomarenko and Popov, 2016).

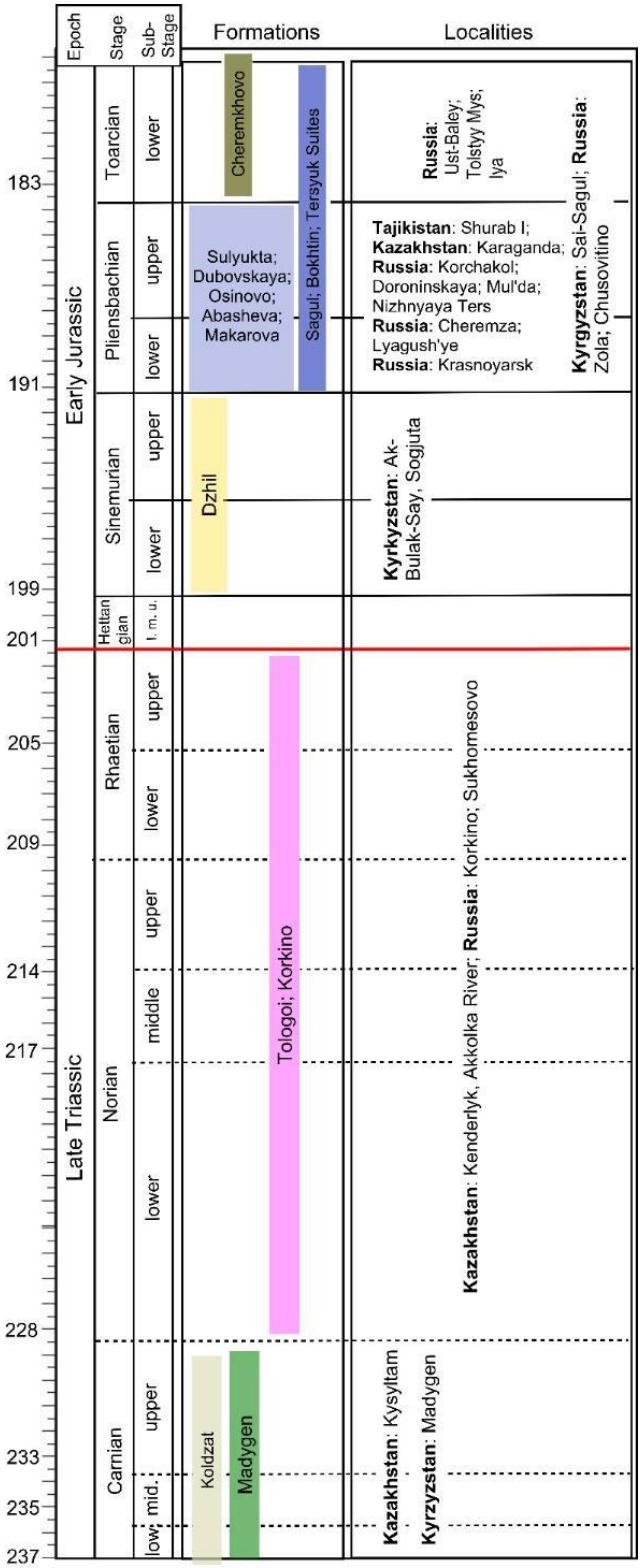

Figure 2.16. Stratigraphic chart of Northern/Central Asian insect-bearing formations and localities.

The Sagul (=Sogul) Formation of Sai-Sagul near Shurab in the Osh Region of Kyrgyzstan (Pritykina, 1970), also known as 'Shurab 3' or 'Svodovoe Ruslo' has produced at least 670 specimens (Sukacheva and Rasnitsyn, 2004). Kuzichkina et al. (1958) considered the formation to be middle–Upper Liassic and Aliev et al. (1981) considered the formation to be late Early Jurassic based on an analysis of the palaeoflora. Sukacheva and Rasnitsyn (2004) discussed the insect assemblages of this formation and concluded that the species were too endemic and the genera either too endemic or too widely distributed to be useful for estimating an age within the general upper Lower–early Middle Jurassic age of the surrounding deposits. This age has been followed by, e.g. Shcherbakov (2008b), Wang et al. (2009), Aristov (2011), Khramov (2014), and Khramov and Makarkin (2015). The formation has been mentioned as Middle Jurassic (Wu and Huang, 2012) or Toarcian (Nicholson et al., 2015, suppl. mat.), without discussion; or as Toarcian–Upper Jurassic Oxfordian based on assemblages of fossil wood, plants, and insects (O'Reilly et al., 2015).

Although insect assemblages have been used to correlated and date formations in this region, the assemblage of the Sagul Formation is not very informative in this regard (Sukacheva and Rasnitsyn, 2004). According to the PBDB, there are only two species shared between the Sagul Formation and Early Jurassic formations (*Shurabiola nana* and *Shurabia parvula*) but only one shared with the Middle Jurassic (*Cicadocoris abditus*) (see Popov, 1985). The insect-bearing horizon occurs in the upper beds of the formation containing aleurolites with seams of brown-grey clays (Khramov and Makarkin, 2015). If the formation does span into the Middle/Upper Jurassic, then it is possible that any beds in the upper part of the formation lie in the Middle Jurassic, either way it is not possible to precisely assign them to stage.

Insects have also been collected from the Dzhil Formation of Sogyuty, Ak-Bulak-Say, Issyk-Kul, Kyrgyzstan (Popov, 1982; Rasnitsyn, 1982), with at least 1500 from Series H, known as the "green shale series" (Martynova, 1943) which is generally thought to be Lower Lias in age based on macro- and microfloral assemblages (Genkina, 1966) and spore pollen analysis (Aliev et al., 1981). It was considered to be Middle to Upper Jurassic based on comparisons of the flora with Chinese floras (O'Reilly et al., 2015, suppl.). This study suggests that the presence of *Neocalamites carrerei, Todites, Cladophlebis*, and *Czekanowskia rigida* in both the Dzhil Formation and the Haiffangou and underlying Beipiao formations of China. The age of the Madygen Formation was considered to range between the Haiffangou and Guojiadian formations based on a lower similarity between the Madygen Formation and the Guojiadian Formation, which sits 'two units' below the Beipiao Formation. Their youngest estimate is based on the age of the lower boundary of the Lanqui Formation which overlies the Haiffangou Formation (Oxfordian). Their oldest is based on similarities between the bivalve assemblage of the Guojiadian Formation with that of the Yanshiping Group, and then the potential age range of dinocysts found in this group (Middle Jurassic: Callovian/Bathonian boundary).

This age is unlikely based on a suite of evidence both from China and Central Asia. Firstly, the Beipiao Formation lies in the middle of O'Reilly et al.'s estimated age range underlying the Haiffangou Formation. U-Pb ages of zircons collected from sandstones in the Beipiao Formation ranged from 233.8 ± 4.2 to 194.3 ± 2.9 Ma (Yan et al., 2005) (Late Triassic to Early Jurassic), suggesting that similarities between this formation and the Dzhil Formation could indicate an Early Jurassic age for the latter, and that the Guojiadian Formation is Early Jurassic or older as it is generally considered (Deng et al., 2017).

Concerning the Central Asian evidence, there is abundant literature regarding the palaeofloras of Mesozoic Central Asia. In regard to the specific taxa O'Reilly et al. (2015) discussed, *Neocalamites carrerei* is recorded in Central Asia from the Late Triassic (Dobruskina, 1995; Mogutcheva, 2009, 2014). The genus is further known outside of the region from the Permian (DiMichelle et al., 2001) to the Jurassic/Cretaceous (Van Konijnenburg-van Cittert and Bandel, 2001; Kiritchkova et al., 2017). *Czekanowskia rigida* is recorded in Central Asia from the Early–Middle Jurassic (Mogutcheva, 2009, 2014; Frolov et al., 2017). Furthermore, Kiritchkova et al. (2017) consider the presence of *C. rigida* alongside *Neocalamites* as indicative of the Early Jurassic. *Todites* is found in Central Asia from the Triassic (Dobruskina, 1982), Early Jurassic (Mogutcheva, 2009; 2014), and Middle Jurassic (Markovich, 1971), but is also known outside of the region from the Permian (Guskov et al., 1980). *Cladophlebis* is known in Central Asia from the Late Triassic (Dobruskina, 1995) and the Early–Middle Jurassic (Mogutcheva, 2009; 2014; Frolov et al., 2017). It is also known outside of the region from the Permian (Durante, 1976) to the Cretaceous (Spicer et al., 2002). A Middle–Upper Jurassic age is therefore unlikely, at least based on correlations with distant formations that are also not precisely understood, and certainly not if the Beipiao Formation is indeed Early Jurassic as the zircon ages suggest.

It is difficult to offer any exact inferences based on these assemblages, but it seems prudent to incline towards the palaeobotanical evidence from the same region as the formations under scrutiny, rather than Chinese formations. Therefore, we regard the formation to lie in the Lower Lias based on the micro- and macrobotanical evidence offered from the region. The insect-bearing horizon occurs in the upper beds of the formation in coal-less, thin, pinkish-yellow and greyish-green laminated clays known as green shales with little in the way of plant material (Khramov and Makarkin, 2015) and so even if the formation spans the Lower Lias the insect horizon lies in the upper part of this range, probably in the Sinemurian as considered by Lukashevich et al. (1998), Rasnitsyn and Quicke (2002), and Krzemińska and Lukashevich (2018).

Mongolia.—Insects have been collected from the Zhargalant Formation of Dzhargalant and Oshin-Boro-Udzur-Ula (Sinitshenkova, 1985). There are two assemblages known from this locality, one

considered to be Lower Jurassic Toarcian based on similarities with Ust-Baley, and another considered to be Middle Jurassic: Bathonian (Rasnitsyn and Quicke, 2002).

Russian Federation.—Insects from Siberian Russia were collected from the Abasheva Formation of Cheremza and Lyagush'ye, Kemerovo (Vishniakova, 1983; Sinitshenkova, 1985); the Osinovka (=Osinovo) Formation of Central Mul'da and Doroninskaya (Ponomarenko, 1985), Korchakol, Kemerovo (Sukacheva, 1985), and Nizhnyaya Ters', Kemerovo (Sinitshenkova, 1985); the Makarova Formation of Krasnoyarsk (Kalugina and Kovalev, 1985); and the Cheremkhovo Formation of Iya (Arnoldi et al., 1977) and Ust-Baley, Irkutsk (Martynov, 1927).

The age of the Abasheva, Osinovka, and Tersyuk Suites formations of the Kuznetsk Basin, southwest Siberia were estimated based on the taxonomic composition of floras (Kiritchkova et al., 2005). The Abasheva Formation was considered to be Pliensbachian with its upper boundary at the Pliensbachian/Toarcian boundary, overlaid by the Osinovka Formation which spans to the Aalenian/Bajocian boundary, this is in turn overlain by the Tersyuk Suite Formation which is entirely Middle Jurassic. Whereas, other assessments of palaeoflora have suggested that the upper Osinovka Subformation is upper Pliensbachian with elements of later [Toarcian] floras (Mogutcheva, 2009). Rare Cycadophyta are recorded which are typically absent from Aalenian deposits (Mogutcheva, 2014). The lower Osinovko Subformation was therefore considered to be lower Upper Pliensbachian and the Abasheva Formation uppermost Hettangian/Sinemurian to Lower Pliensbachian, probably later in this estimation based on similarities with the assemblage of the middle Cheremkhovo Formation (Frolov et al., 2017). Despite a dearth of plant remains (Teslenko, 1970) The lower subformations of the Makarova Formation were similar to the Hettangian–Sinemurian palynozones two and three and the middle Makarova, where the insects are found, to Pliensbachian palynozones.

The Cheremkhovo Formation of the Irkutsk Basin is quite productive for insects with 85 species being described from the formation according to the Palaeobiology Database (PBDB). It has been described as being characteristic of a lacustrine/boggy environment (Panov and Baraboshkin, 2015). The insects were collected from the upper beds of the formation known as the upper Subformation, or Ust-Baley Member in lenses of thinly laminated yellowish grey mudstones interbedded with dark grey siltstones within pale grey sandstones (Akulov et al., 2015). The formation is generally considered to be Middle to late Early Jurassic and has been considered as: Pliensbachian–Toarcian (Odintsova, 1977; Shurygin and Ankudimova, 1981), Pliensbachian–Aalenian (Kiritchkova and Travina, 2000), Pliensbachian (Skoblo et al., 2001), Aalenian (Rasnitsyn and Quicke, 2002), and Toarcian (Kiritchkova et al., 2005).

More recently there have been several studies attempting to come to a resolution on the age of this formation. Akulov et al. (2015) considered the Cheremkhovo (=Cheremkhovskaya) Formation to range

from the Pliensbachian–Toarcian based on palaeobotanical evidence from Shurygin and Ankudimova (1981) and (Frolov, 2013), with the upper Subformation around the upper Lower Toarcian to the middle Toarcian. Panov and Baraboshkin (2015) consider the upper Cheremkhovo Subformation to correspond to the Kamalin complex which, on the basis of floral and palynological assemblages, ranges from the Toarcian–Aalenian. Mikheeva et al. (2017) did not examine the Cheremkhovo Formation in detail but considered it to be Pliensbachian–Early Toarcian, correlating with the Dabat Formation of the Baikal Group. An in-depth assessment of palaeobotanical assemblages with comparisons of flora between Siberia and other global assemblages from the Early and Middle Jurassic by Kiritchkova et al. (2017) suggested that the formation spans from the uppermost Pliensbachian to the Lower Aalenian, with the upper Subformation lying completely within the Lower Aalenian. Frolov et al. (2017) carried out a lithological and palaeobotanical analysis of sediments in the Irkutsk Basin and concluded that the lower Cheremkhovo Subformation lies in the Pliensbachian, up to the lower boundary of the Toarcian, the middle Subformation in the lower to middle Toarcian, and the upper Subformation in the upper Toarcian.

The age estimates are consistently within the middle/upper Lower Jurassic and/or lower Middle Jurassic, with the upper Subformation (which contains the insect-bearing horizon) between the upper Toarcian and Lower Aalenian. The Cheremkhovo insect assemblage has 10 species and 32 genera in common with the Early Jurassic assemblages and only four species and 16 genera in common with the Middle Jurassic insect assemblages. Furthermore, all of the 16 genera shared with the Middle Jurassic range from the Early Jurassic including some genera that range back to the Triassic. Most of the shared species are found in the Abasheva, Makarova, Sagul, and Sulyukta formations of Russia, Kyrgyzstan, and Tajikistan, three of which are considered Pliensbachian in age and the other is considered Pliensbachian–Toarcian. It would seem prudent, therefore, based on the insect data, to consider an Early Jurassic age for the Cheremkhovo Formation, probably Toarcian based on the combination of evidence from palaeobotanical and palaeoentomological assemblages.

Tajikistan.—The Sulyukta (=Sulyucta) Formation is generally considered to be Early–Middle Jurassic (Rasnitsyn and Quicke, 2002; Makarkin et al., 2014). The formation is abundant in the Early Jurassic Reculida genus *Shurabia* (Aristov et al., 2009). It has been listed as Pliensbachian (Qiao et al., 2013) and Middle Jurassic (Philippe et al., 2013; Wan et al., 2016). There have been no comprehensive assessments of the assemblages, so it is difficult to ascertain an age. There are seven insect species/genera in common with the Early Jurassic and two species/genera in common with the Middle Jurassic according to the PBDB, which could suggest a later Early Jurassic age.

2.6 GONDWANA

Australia.—Most Late Triassic insects from Australia are found in the Blackstone and Mount Crosby formations of the Ipswich Coal Measures in Queensland (Fig. 2.17) which were thought to be of Carnian age (Scott et al., 2004). The Mount Crosby Formation is underlain by the Brisbane Tuff for which Purdy and Cranfield (2013) reported an unpublished U-Pb zircon SHRIMP age of 226 ± 2 MA, above the Carnian/Norian boundary (Ogg et al., 2016). Therefore, any formations above the Brisbane Tuff can be considered as younger than Carnian. The Blackstone Formation is the uppermost formation in the Ipswich Coal Measures and is overlaid by the Aberdare Conglomerate Member (Bundamba Group: Woogaroo Subgroup). The Aberdare Conglomerate is considered to be Rhaetian (Rozefelds, 1985) with the Norian/Rhaetian boundary lying unconformably at its lower boundary (Jansson et al., 2008). The insect-bearing horizon from the Blackstone Formation (known as the Denmark Hill insect bed) is described as lying equidistant between two of the uppermost coal seams (Tindale, 1945) and containing abundant fossils of the fern *Thinnfeldia* (junior synonym of *Pachypteris*, according to Doludenko (1974). The Mount Crosby insects are collected from the lower beds of the Mount Crosby Formation, 20 feet above its LB (Tindale, 1945). It would therefore be reasonable to assume a late Norian age for the insects from the Denmark Hill insect horizon and an early Norian age for insects found in the lower Mount Crosby Formation horizon.

Fossil insects were also found in Tasmania, from the New Town Coal Measures (Riek, 1962) and the Mt. Nicholas Coal Measures (Riek, 1967). The former fossils were collected from a grey mudstone also containing ferns, approximately ‘3 feet’ (~0.91 m) below a coal seam overlain by feldspathic sandstone. The coal-bearing feldspathic sandstones of New Town are considered as Late Triassic (Bacon and Everard, 1981). The exact horizon of the Mt. Nicholas insect is not specified, but the unit has been said to correspond to the New Town Coal Measures (Collinson et al., 1990). Therefore, the Tasmanian insects are probably Late Triassic in age. There are several other localities which bear similar aged insects, but they are either not very productive or are difficult to date accurately. Several insects have been collected from the Aberdare Conglomerate Member of Rhaetian age (Rozefelds, 1985) and one insect is published from the Tivoli Formation (Lambkin, 2016) which underlies the Blackstone Formation and so is also Norian. Several poorly preserved insects have also been collected from the Wianamatta Shales of St. Peters near Sydney (Riek, 1970), but there is little information regarding exact horizons, and they are considered as Late Triassic or possibly Jurassic (Riek, 1970).

Early Jurassic insects are also known from the Mintaja insect locality (Hill River) of the Cattamarra Coal Measures of Western Australia (Riek, 1968; Martin, 2008a, 2008b). This formation is dated as Sinemurian–Toarcian and Martin (2008a) provides an in-depth discussion on these localities. The nature of the insect-bearing outcrops means that correlation with other sections is difficult, and so the exact level of the insect horizon is difficult to ascertain.

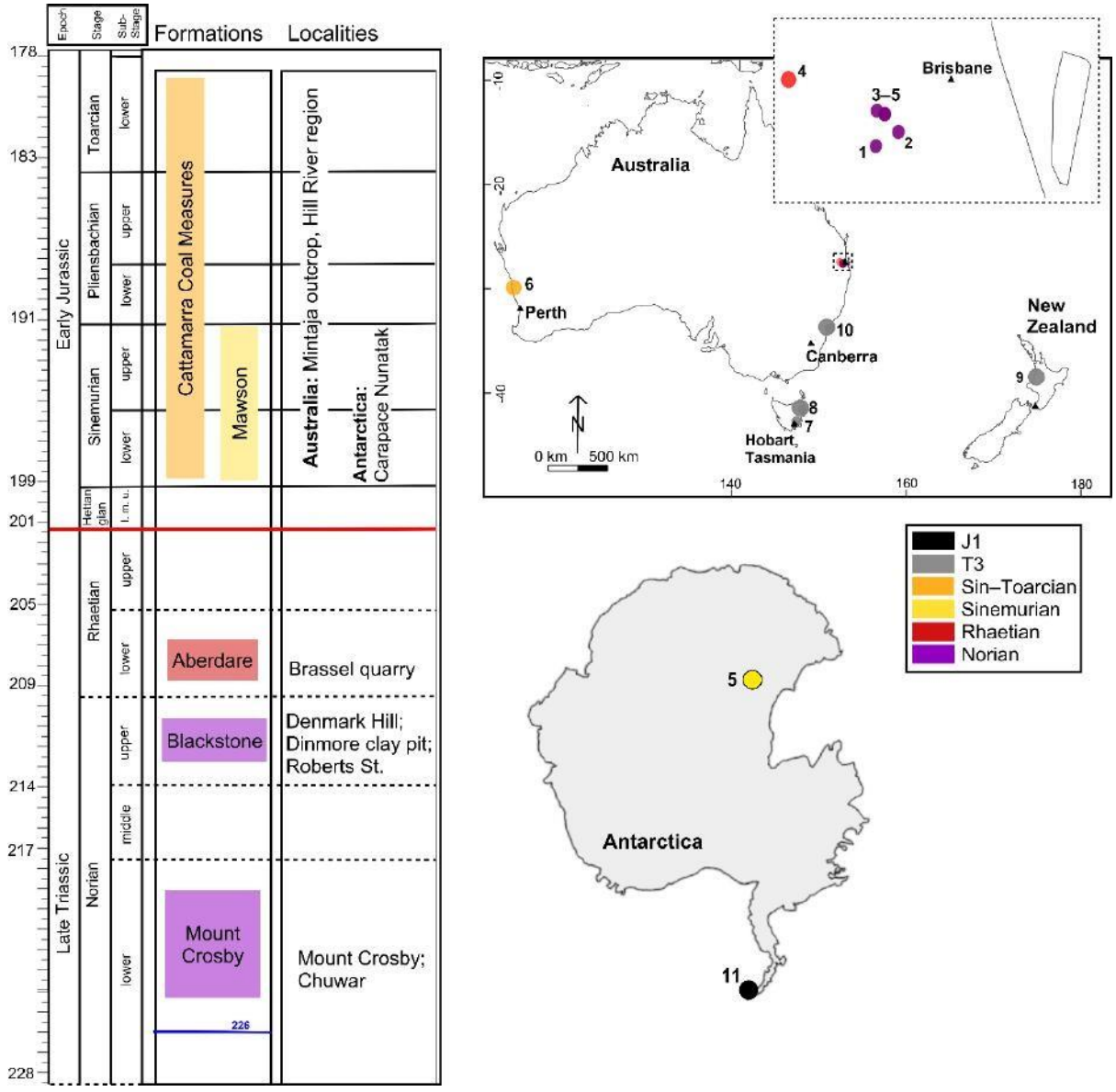

Figure 2.17. Map of Late Triassic to Early Jurassic insect-bearing localities of Australia, New Zealand and Antarctica with stratigraphic column. Localities are: 1. Denmark Hill insect bed; 2. Denmark Hill, 'new outcrop'; 3. Dinmore clay pit (including Roberts Street); 4. Mount Crosby insect locality; 5. Chuwar.

New Zealand.—A beetle elytron has been recorded from a horizon in New Zealand which is probably Late Triassic. The beetle is mentioned briefly in Craw and Watt (1987) as being of Triassic age. Although the original thesis was not available there was a subsequent paper (Grant-Mackie, 1959). This paper does not mention the beetle specimen explicitly, but it does state that the lowest rocks of the study area. where the beetle was collected, were of early Carnian age.

Antarctica.—The Mawson Formation has produced a dragonfly wing from Carapace Nunatak, which is located in South Victoria Land, Antarctica. The insect was originally described by Carpenter (1969) and was redescribed and the locality discussed in Kelly and Nel (2018a) (see Appendix 2). Schülter

(2003) also reported the specimen but gave no further insights into its age although it has been considered Middle Jurassic (Elliot, 2000), earlier authors had discussed the similarity of conchostracans found in the same deposits with older faunas from South Africa (Borns et al., 1972). The Mawson Formation was formed by a pyroclastic event from the Hettangian to Lower Pliensbachian based on evidence from U/Pb and $^{40}Ar/^{39}Ar$ dating of volcanic rocks in North Victoria Land (Musumeci et al., 2006). In South Victoria Land, there is a hiatus in the Early Jurassic (Schöner et al., 2011) below the insect-bearing horizon, and the Mawson Formation is overlaid by the Carapace Sandstone Formation, which is Upper Sinemurian to Lower Pliensbachian (Ribecai, 2007). Therefore, the horizon from which the dragonfly was collected is possible of Sinemurian age.
Two species of beetle were described by Zeuner (1959a) from Mount Flora, Hope Bay, Grahamland. Based on the poorly preserved beetles, Zeuner estimated an age between the Late Triassic and Jurassic. The Hope Bay floras have been estimated to be Early Jurassic based on comparisons with floras from Argentina (Rees and Cleal, 2004). Liverworts have been collected from shale layers from Mount Flora in the Flora Glacier Member of the Mount Flora Formation (Ociepa, 2007) and the Early Jurassic age was not disputed. A more detailed report indicated that shale layers were only prevalent in the Flora Glacier Member (Birkenmajer and Ociepa, 2008) indicating a possible late Early Jurassic age for shale layers from Mount Flora.

India.—Two localities in India have insect horizons estimated to lie in the Early Jurassic, but the evidence is not compelling and further stratigraphic work is needed to determine their ages. The Kota Formation of Sirpur Taluka and andhra Pradesh, India is considered to be Early Jurassic (Mostovski and Jarzembowski, 2000), even though earlier authors suggested that the upper beds may be Middle Jurassic based on ostracod assemblages (Misra and Satsangi, 1979). An Upper Lias age was suggested based on palynological content (Vijaya, 2000) and by the presence of a flying reptile known from the German Upper Lias (*Campylognathoides*) (Yadagiri, 2001) but there is little other evidence. The underlying Dharmaram Formation is also suggested to be Early Jurassic based on comparisons of fossil assemblages (Mukhopadhyay et al., 2010). Most of the evidence points towards a late Early Jurassic possibly middle to Upper Lias age for the formation.

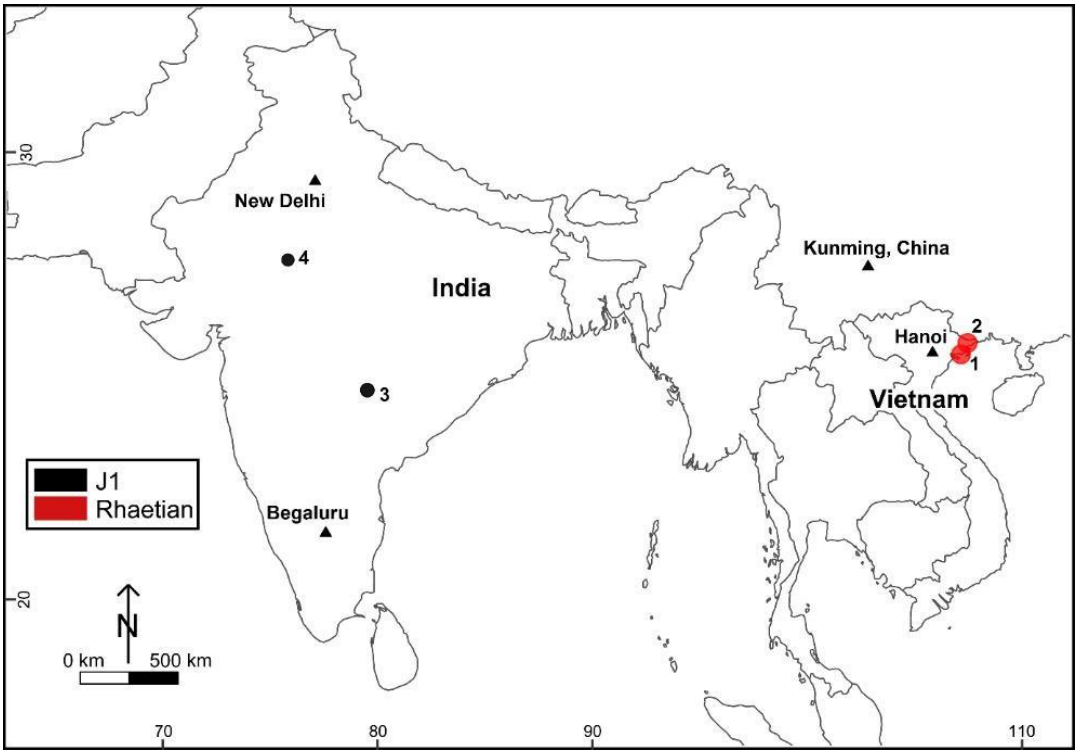

Figure 2.18: Late Triassic to Early Jurassic insect-bearing localities of South and South-East Asia. Localities are: 1. Hongay mine, Vietnam; 2. Keboa mine, Vietnam; 3. Sirpur Taluka, India; 4. Kota Formation outcrop k-2.

Vietnam.—Three cockroach wings were collected from a coal formation in Hongay of lower Tonkin (Fig. 2.18) by Zeiller (1903), who considered them to be Rhaetian in age. Although there have been other suggestions, recent authors have also suggested that fossils from this area are Rhaetian (Vozenin-Serra and Franceschi, 1999; Vaez-Javadi and Allameh, 2015). It is not clear exactly which section yielded the insects, and so it is difficult to correlate with later literature, but they are at least Late Triassic and possibly Rhaetian in age.

South Africa and Lesotho.—Late Triassic insects of South Africa and Lesotho are found in the Molteno Formation (Karoo Supergroup: Stormberg Group). This formation is the lowest in the Stormberg Group and unconformably underlies the Elliot Formation, which spans the TJB (Rubidge et al., 2016). The upper boundary of the Molteno Formation has been radiometrically dated to ~215+5 MA (anderson and anderson, 1984) which is considered mid-Norian (Ogg et al., 2016); the lower boundary has been radiometrically dated to ~230MA (Catuneanu and Elango, 2001) which is considered Lower Carnian. Insects from this formation are usually recorded as Carnian (Wappler, 2001), but this depends on where exactly in the Molteno Formation's stratigraphy the insect-bearing horizons lie.

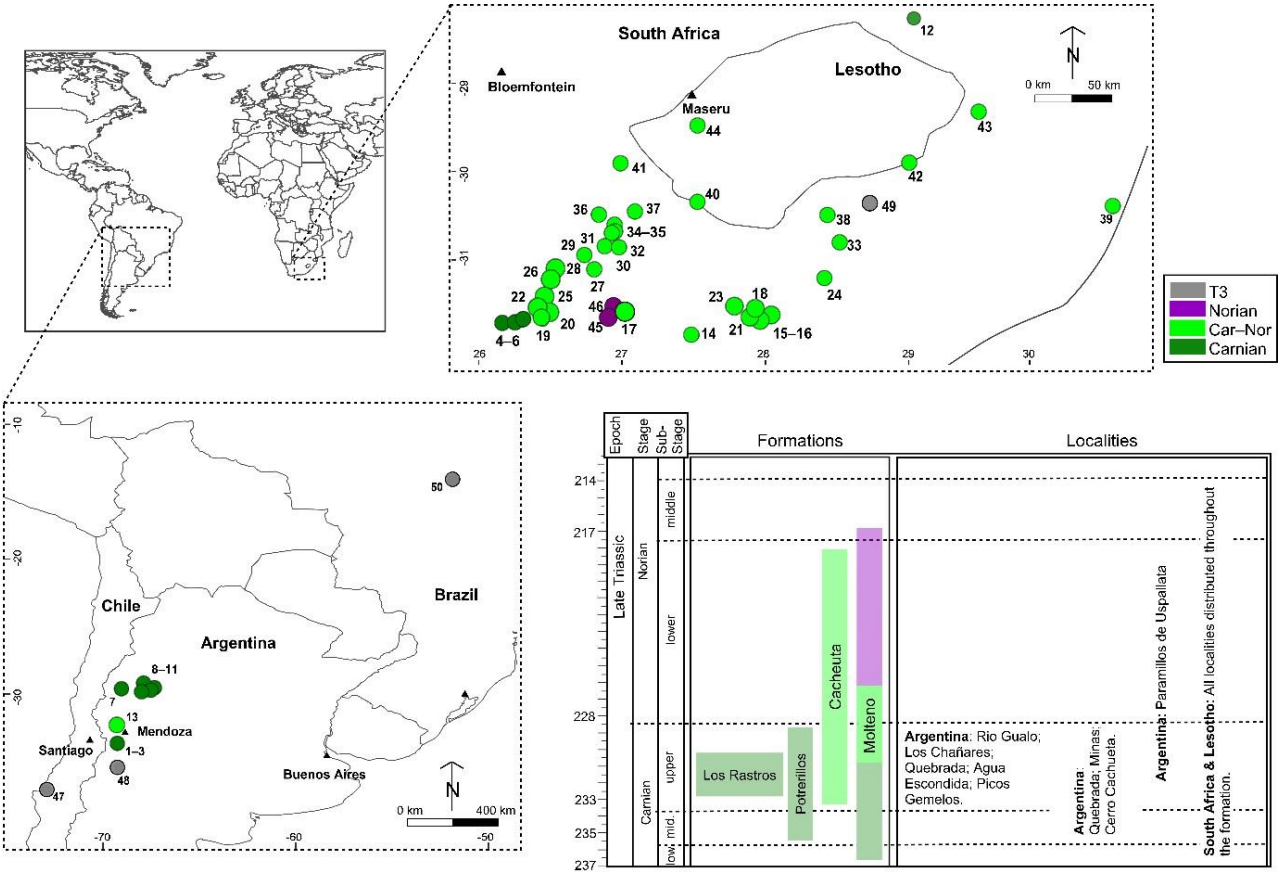

Figure 2.19: Insect-bearing horizons from South Africa/Lesotho and South America, locality is South Africa unless otherwise stated. 1–3. Quebrada del Durazno; Minas de Petroleo; Agua de las Avispas, Argentina; 4–6. Aasvoelberg (Aas 111, 211 & 611); 7. Quebrada de Ischichuca, Argentina; 8–11. Rio Gualo (5th cycle), Los Chañares (1st cycle), Agua Escondida (4th cycle), Picos Gemelos (5th cycle), Argentina; 12. Little Switzerland (Lit 111); 13. Paramillos de Uspallata, Argentina; 14. Askeaton; 15–16 Pen (311, 411); 17. Greenvale (Gre 121); 18. Konings Kroon (Kon 222); 19. Cyphergat; 20. Boesmanshoek Pass (Boe 112); 21. Kannaskop (Kan 112); 22. Molteno (Mol 111); 23. Navar (Nav 111); 24. Waldeck (Wal 111); 25. Klein Hoek (Kle 111); 26. Kapokkraal; 27. Kommandantskop (Kom 111); 28. Telemaghus Spruit (Tel 111); 29. Elandspruit (Ela 111); 30. Kraai River (Glenburn) (Kra 311); 31. Kraai River (Kra 111); 32. (Lut 511), (Lut 411); 33. Tina Bridge; 34–35. (Lut 111); 36. Nuwejaarspruit (Nuw 211); 37. Winnaarspruit (Win 111); 38. Mount Fletcher; 39. Umkomaas; 40. Qualasi Hill; 41. (Gol 111); 42. Qachasnek (Qac 111); 43. Hlatimbe Valley (Hla 213); 44. Mazenod, Lesotho; 45. Birds River (Bir 211); 46. Birds River (311); 47. Santa Juana, Chile; 48. Arroyo Llantenes, Argentina; 49. Siberia; 50. Brazil.

Insects have been found at 43 localities in South Africa and Lesotho (Fig. 2.19). Two were particularly prolific, Birds River, South Africa (Bir 111) and Mazenod, Lesotho (Maz 211), with 474 and 372 specimens respectively. Five further localities have produced over 100 specimens each: Kapokkraal (Kap 111), Umkomaas Valley (Umk 111), Aasvöelberg (Aas 311 and Aas 411) and Little Switzerland (Lit 111) (anderson et al., 1998). The horizon at Bir 111 is found in cycle 5 of Turner

(1983) and anderson and anderson (1983, 1984), 80 m from the UB of the formation (Cairncross et al., 1995) possibly in the Tsomo Member which underlies the Elliot Formation (Bordy, 2005). The horizon at Maz 211 was found in an unnamed shale horizon of cycle 2 immediately overlying the Little Bamboo Mountain Shale Member near the top of the Indwe Sandstone Member (anderson and anderson, 1983, 1989). The horizon at Kap 111 is not mentioned by anderson and anderson (1983, 1989), but according to Cairncross et al. (1995) it lies about 180 m from the LB of the Molteno Formation. At Umk 111 the horizon is found in cycle 2 in the Little Bamboo Mountain Shale Member (anderson and anderson, 1983, 1989), 120 m from the LB of the formation (Cairncross et al., 1995). Aas 311 and Aas 411 are not mentioned by anderson and anderson (1983, 1989) either, but the horizon at Aas 111 is found near the very bottom of the section in 'cycle 1–2' directly underlying Lit 111 of the shale lens at the base of the Indwe Sandstone Member (anderson and anderson 1983, 1989), 40–100 m from the LB of the formation (Cairncross et al., 1995).

Given the positions of the insect-bearing horizons, it seems evident that not all insects from the Molteno Formation are Carnian. Those from horizons near the top of the formation (e.g. Bir 111) are likely to be lower-Middle Norian whereas those near the bottom (e.g. Aas and Lit 111) are likely to be lower-Middle Carnian. Those towards the middle of the formation are more difficult to estimate but probably lie around the Carnian/Norian boundary. The majority are within the Indwe Sandstone Member, and so more accurate dating of this member will bring about more accurate ages for these insects. Further specimens have also been described from the Cave Sandstone of Siberia (South Africa) (Haughton, 1924). These few fragmentary pieces were collected from a shale band near the base of the sandstone which is described as overlying red beds. The Cave Sandstone is considered Carnian to Norian (Keyser, 1973). It is not clear how this horizon correlates with the Molteno horizons.

South America.—There are several insect-bearing horizons in the South American Triassic (Fig. 2.19). The most prolific are found in the Los Rastros and Potrerillos formations of Argentina, with additional material from the Cacheuta and Llantenes formations of Argentina, the Santa Juana Formation of Chile and the Caturrita Formation of Brazil. The Los Rastros Formation is part of the Agua de la Peña Group and overlies the Chañares Formation, of which at least the upper beds are Lower Carnian based on radiometric dating of tetrapod-bearing levels (Marsicano et al., 2016). A bed lying in the middle of the formation has been dated to 233.7 ± 0.4 Ma, putting the upper boundary of the Chañares Formation in the Upper Carnian. Overlying the Los Rastros Formation is the Ischigualasto Formation, the lower beds of which have been radiometrically dated to 231.4 ± 0.3 Ma (Mancuso et al., 2014). Insects are found in the lower shales of the formation (Martins-Neto et al., 2006) and so are Upper Carnian in age.

The Potrerillos Formation is part of the Uspallata Group overlying the Las Cabras Formation and unconformably underlying the Cacheuta Formation. Tuffs in the lower beds of the Potrerillos Formation have been SHRIMP dated to 239 ± 4.5 Ma (Spalletti et al., 2008), placing them in the upper

Ladinian. Beds in the middle of the Potrerillos Formation have been radiometrically dated to ~235 Ma (Cariglino et al., 2016) probably putting the UB somewhere in the Upper Carnian. Insects are found in the upper beds of the Potrerillos Formation (Martins-Neto et al., 2003; Lara and Aristov, 2017) and so are Carnian in age, probably middle–late Carnian based on the Upper Carnian to early Norian position of the Cacheuta Formation (Lara and Wang, 2016). Several insects have been found in the Llantenes Formation of Argentina (Brauckmann et al., 2010), the Santa Juana Formation of Chile (Martins-Neto et al., 2003, 2006), and the Santa Maria Formation of Brazil. These formations are generally considered to be middle to Late Triassic in age, and no further information relating to the insect-bearing horizons was found. It was previously thought that the insects described from the Norian of South America constituted the only Norian-aged entomofauna from the Southern Hemisphere (Brauckmann et al., 2010). At the time this was true as other Southern Hemisphere insect localities were considered Carnian but as the Triassic timescale continues to be refined it becomes clear that many Gondwanan insect localities are more similar in age than previously thought.

Chapter 3. Taxonomic revision of British Late Triassic and Early Jurassic insects

3.1 Introduction

Most of the insects in the British collections are from historical collections and have not been taxonomically revised recently. Upon initial assessment of the collections it was clear that the species- and genus-level taxonomy required revision for most groups. Presented in this chapter are the results of these taxonomic revisions. It is not an entire systematics for the British TJB insects but rather a presentation of the taxonomic changes made to the British record in the dataset used for the diversity analysis in subsequent chapters. Taxonomic accuracy of the fossil record is important to ensure that datasets represent biocenoses as accurately as possible. It has been argued that taxonomic revision is not necessary for estimating macroevolutionary or macropalaeoecological trends so long as the data are sufficiently numerous (Sepkoski, 1992). Wider experience, however, is that unrevised datasets can give misleading results due to errors in taxonomy or in dating of fossils (Benton et al., 2013). Other authors have argued in favour of taxonomic revision as a necessary step in understanding past faunas and floras (Maxwell and Benton, 1990; Grimaldi, 2001; Lucas and Tanner, 2018).

It is also important to considered different taxonomic levels when investigating changes through time. As discussed in Chapter 1, an extinction signal may not always be expressed at higher levels. Species-level analysis for insects has been advocated for (Ross et al., 2000; Nel and Prokop, 2009). Furthermore, Nicholson et al. (2015) suggested looking at lower taxonomic levels to reveal signals not caught in their family-level analysis. We therefore provide species- and genus-level taxonomic revisions of the British Late Triassic/Early Jurassic insects to test for an extinction level at lower taxonomic levels.

3.2 Materials and methods

Repositories and institutional abbreviations.—BELUM, National Museum of Northern Ireland; BRSMG, Bristol Museum & Art Gallery; BGS, British Geological Survey, Keynsham; BXMNH, Museum of Natural History, Brussels; CAMSM, Sedgewick Museum, Cambridge; CHAGM, Wilson Museum, Cheltenham; EMAUG, Ernst-Moritz-Arndt Universität, Greifswald; ETH, Swiss Federal Institute of Technology, Zurich; GCMAG, Gloucester Museum; LEICT, New Walk Museum & Art Gallery, Leicester; LXMNH, Luxembourg Museum; MANCH, Manchester University Museum; MCZ, Museum of Comparative Zoology, Harvard University; MNEMG, Maidstone Museum; NHMUK, Natural History Museum, London; MNHN, Muséum national d'Histoire naturelle, Paris; NIGPAS, Nanjing Institute of Geology and Palaeontology of the Chinese Academy of Sciences; NMS, National Museums Scotland; NMW, National Museum Wales; OUMNH, Oxford University Museum of Natural History; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow; SRMNH, Swedish Royal Museum of Natural History; TTNCM, Somerset Heritage Centre for Taunton Museum; USNM, Smithsonian Institute, Washington DC; VMNH, Virginia Museum of Natural History, Martinsville; WARMS,

Warwickshire Museum; WCAGM, Worcester Museum; YORYM, Yorkshire Museum; YPM, Yale Peabody Museum, New Haven.

Declaration regarding papers published from and included in this thesis.—The descriptions of new taxa in this thesis are not official descriptions and have been, are being, or will in due course be published in official journals. In compliance with the International Code of Zoological Nomenclature recommendations (Section 8: Recommendation 8a) any new taxa described below have been or will be included in the official Register of Zoological Nomenclature (ZooBank) and LSIDs have been provided. The following chapter includes the systematic descriptions from five papers that were published during the course of this project. They were not each included as a chapter as this would have disrupted the cohesiveness of the thesis. Rather, the systematic descriptions are included here verbatim but with consistent formatting, and the papers are included as appendices. Also, each figure is captioned with the published figure citation and the appendix to find it in. >85% of the work for each paper was my own, the rest was co-authors supporting my work.

Odonata are discussed in section 3.3.1. The Systematic Palaeontology section including the descriptions for the family Campterophlebiidae are from Kelly and Nel (2018b, pp. 88–92) (see Appendix 1) and the Systematic Palaeontology section including the descriptions of the families Liassophlebiidae and Anglophlebiidae are from Kelly and Nel (2018a, pp. 3–12) (see Appendix 2). For these papers, I organised a training course on Odonata morphology with andré Nel at the MNHN. I examined all specimens first-hand at NHMUK and WARMS, prepared all figures, made all taxonomic decisions, and prepared, wrote, and submitted the manuscripts. Nel provided expert advice and training on odonate morphology and taxonomy. Dermaptera are discussed in section 3.3.2, and the Systematic Palaeontology section including the descriptions of the species in this order is taken from Kelly et al. (2018b, pp. 5–11) (see Appendix 3). I examined all specimens first-hand at NHMUK, OUMNH, TTNCM, MCZ, and USNM, prepared all figures, made all taxonomic decisions, and prepared, wrote, and submitted the manuscript under the supervision of andrew Ross. I also presented this paper at the International Conference on Fossil Insects, Arthropods and Amber, 2016. Edmund Jarzembowski provided additional specimens not relevant to this project. The coleopteran genus Holcoptera is discussed in section 3.3.6. The Systematic Palaeontology section including the descriptions of the species in this genus are from Kelly et al. (2017, pp. 5–13) (see Appendix 4). I examined all specimens first-hand at NHMUK, NMW, YORYM, WARMS, BRSMG, USNM, MCZ, and YPM, prepared all figures, made all taxonomic decisions, and prepared, wrote, and submitted the manuscript under the supervision of andrew Ross. Philip Davidson provided a specimen for description (NHMUK PI II.3101 a&b, Fig. 3.54) and advice on the geology of the local area. The trichopteran family Necrotauliidae is discussed in section 3.3.9. The Systematic Palaeontology section including the descriptions of the species in this family are from Kelly et al. (2018a, pp. 5–10) (see

Appendix 5). I examined all specimens first-hand at NHMUK, YORYM, OUMNH, TTNCM, EMAUG, NIGPAS, and PIN, prepared all figures, made all taxonomic decisions, and prepared, wrote, and submitted the manuscript under the supervision of andrew Ross. Robert Coram provided specimens for description (NHMUK II 3103 a&b, Fig. 3.65).

Most other descriptions provided herein are in the process of being published. Orthoptera are discussed in section 3.3.3. These descriptions will appear in Kelly and Ross (In preparation a–d). I examined all specimens first-hand at NHMUK, YORYM, WARMS, OUMNH, BGS, LEICT, USNM, and EMAUG, prepared all figures, made all taxonomic decisions, and am writing the manuscripts under the supervision of andrew Ross. Hemiptera are discussed in section 3.3.5. These descriptions will appear in Kelly et al. (In preparation b). I examined all specimens first-hand at NHMUK, CHAGM, and NMW, prepared all figures, made all taxonomic decisions, and am writing the manuscript under the supervision of andrew Ross. Bo Wang provided additional specimens from the Chinese collections. Neuroptera are discussed in section 3.3.7. These descriptions will appear in Kelly et al. (In preparation a). I examined all specimens that appear in this thesis first-hand at NHMUK and OUMNH, prepared both figures, made all taxonomic decisions, and am writing the manuscript with advice from James Jepson under the supervision of andrew Ross. New taxa to be described in these papers are included in this thesis in a generic format, e.g. “Orth:Loc. sp. nov. 1” or “Hem:Proc. sp. nov. 1” to refer to a new species in the orthopteran family Locustopseidae and a new species in the Hemipteran family Procercopidae, respectively.

There are almost 4000 registered insect specimens from the Late Triassic and Early Jurassic of England, most held at NHMUK with additional sizable collections at NMW, BGS, and WARMS. Several smaller collections of British insects collected by Brodie are held in the US at MCZ and USNM and were visited for the project. Collections were also examined at other institutes abroad for comparison where they were relevant to the revision of British taxa, including German material at EMAUG, Swiss material at ETH, Swedish material at SRMNH, US material at YPM, Russian and Central Asian material at PIN, and Chinese material at NIGPAS. Several collections were surveyed electronically to assess specimens: VMNH, BXMNH, and LXMNH. All specimens were examined using the stereomicroscopes available at the different institutes. Specimens were imaged using a digital camera attached to a Leica microscope where possible, or with a Nikon D3300 camera with AF-S Micro Nikkor 40 mm macro lens attached to a stand when a camera/microscope was not available. To best capture the preserved venation of the specimens, light sources were applied at various angles and where applicable a light coating alcohol was used to further highlight venation. Line drawings of each type specimen were prepared using vector drawing tools over photographs in the Serif DrawPlus X8 graphics package. Wherever possible this was carried out at the institute with the specimen to hand to capture any difficult to photograph venation but where this was not possible a suite of photographs was taken with notes to make sure the drawings were as accurate as possible.

3.3 REVISED TAXONOMY

3.3.1 Odonata

This order contains the dragonflies (suborder Anisoptera/Epiprocta) and damselflies (suborder Zygoptera). They are charismatic, medium to large insects with a distinctive general habitus and behaviours, which makes them easily identifiable to order. They have an enlarged thorax for flight muscles, elongate wings with rich venation, and grasping appendages for copulation (Gullan and Cranston, 2010). More specifically, their wings are identified by the presence of a nodus in the anterior margin and an arculus vein, the reduction of the posterior cubital vein (Grimaldi and Engel, 2005). The suborders are similar except that adult damselfly eyes are wide apart and the fore- and hindwings are similar whereas in dragonflies the eyes are either contiguous or only slightly separated, the hind wings are broader than the forewings, and both have characteristic cells known as triangles and hypertriangles (Gullan and Cranston, 2010). Generally, damselflies fold their wings in-line with their abdomen at rest whereas dragonflies hold their wings out at rest (Fig. 3.1) (Grimaldi and Engel, 2005), although this is not always the case.

Several families have been recorded from the British Late Triassic and Early Jurassic, two of which were revised for this study, Liassophlebiidae and Campterophlebiidae. Heterophlebiidae is also recorded but did not require further revision. Liassophlebiidae Tillyard, 1925 was revised by Kelly and Nel (2018a) in which I provided the following introduction to the family (see Appendix 1 for the full account). Liassophlebiidae was initially described for the type genus *Liassophlebia* Tillyard, 1925, which was erected for four species based on fragmentary wings: *L. magnifica* Tillyard, 1925; *L. withersi* Tillyard, 1925; *L. batheri* Tillyard, 1925; and *L. westwoodi* (Hagen, 1850), the latter was based on Brodie (1845, pl. 10, fig. 8), and a further two from abdominal fragments, *L.* (?) *clavigaster* Tillyard, 1925 and *L.* (?) *hopei* (Brodie, 1845), the latter was based on Brodie (1845, pl. 10, fig. 3). Also, an additional genus, *Petrophlebia* Tillyard, 1925 was described. Liassophlebiidae was recently suggested to have originated in the Hettangian and gone extinct in the Toarcian (Nicholson et al, 2015, supplementary data). However, this study did not include the four species from the Rhaetian of England (Tillyard, 1925). When these are included it pushes the age of the family back to before the Triassic/Jurassic boundary.

Petrophlebia was transferred to Campterophlebiidae by Nel et al. (1993), and its position in this family was confirmed by Kelly and Nel (2018b). *P. anglicanopsis* Zeuner, 1962 was described and Zeuner emended the family diagnosis to include those species with a basally closed discoidal cell (Zeuner, 1962). This species was transferred to *Liassophlebia* by Whalley (1985), was then considered of uncertain generic position by Nel et al. (1993) and was recently transferred to Campterophlebiidae by Kelly and Nel (2018b). *L. gigantea* Zeuner, 1962 and *L. jacksoni* Zeuner, 1962 were also described. Whalley (1985) described *L. pseudomagnifica* Whalley, 1985 based on a specimen of *L. magnifica* previously identified by Zeuner.

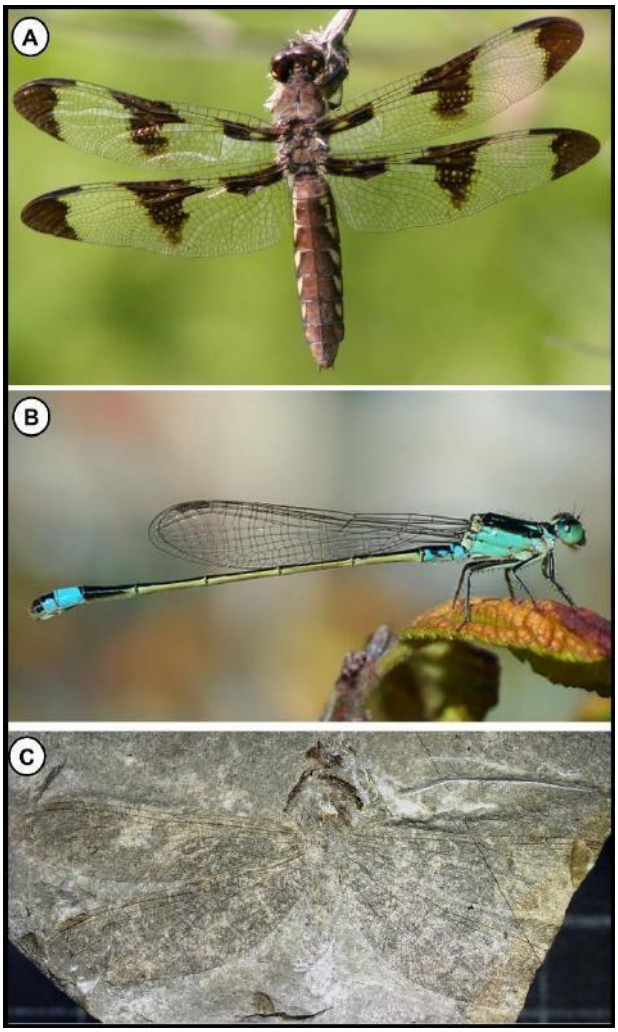

Figure 3.1. Examples of some dragonflies and damselflies of the order Odonata. A. Extant dragonfly, Libellulidae: *Libellula lydia* (photo by R.A. Nonenmacher), B. Extant damselfly, *Ischnura senegalensis* (photo by Laitche), C. Jurassic dragonfly, *Heterophlebia buckmani* (NHMUK 3988).

Systematic Palaeontology

Order ODONATA Fabricius, 1799

Clade ISOPHLEBIOPTERA Bechly, 1996

Subclade ISOPHLEBIIDA Bechly, 1996

Superfamily ISOPHLEBIOIDEA Handlirsch, 1906

Family CAMPTEROPHLEBIIDAE Handlirsch, 1920

Genus LATEOPHLEBIA Kelly and Nel, 2018b

LSID: urn:lsid:zoobank.org:act:32B754E4-74EB-4584-88DA-AAB72C292631

Type species.—*Lateophlebia anglicanopsis* (Zeuner, 1962).

Diagnosis.—Hindwing characters only. Anal vein completely separated from CuA; subdiscoidal area open posteriorly; CuA2 distinctly curved; areas between CuA1 and MP and between MP and MA1 narrow; CuA1 ending well distal of bases of Rs3/4 and IR2, and basal of nodus; Rs3/4 and MA1 nearly straight; only one row of cells in area between MA1 and MP and between MP and CuA1; very few cells in subdiscoidal area below discoidal cell.

Lateophlebia anglicanopsis (Zeuner, 1962)

1962 *Petrophlebia anglicanopsis* Zeuner: pp. 160–161, pl. 24, figs 1–2.

1985 *Liassophlebia anglicanopsis* (Zeuner); Whalley: pp. 122–123, fig. 8a.

1993 *Liassophlebia anglicanopsis* (Zeuner); Nel et al.: pp. 141–142.

Holotype.—NHMUK In.49573 (Fig. 3.2). 'flatstones' (Bed 83) of the Obtusum Zone: Obtusum Subzone (Lias Group: Charmouth Mudstone Formation: Black Ven Mudstone Member); Lower Jurassic: Upper Sinemurian; Stonebarrow, Dorset.

Diagnosis.—Only hindwing characters known. Areas between CuA1 and MP and between MP and MA1 narrow; mostly only one row of cells in areas between MA1 and MP, and between MP and CuA1; very few cells in subdiscoidal area below discoidal cell.

Redescription.—This species is based on the basal two-thirds of a single hindwing. Wing hyaline, preserved part 67.5 mm long and 20.0 mm wide. Wing shortly petiolate; anal area poorly preserved but with irregular cells, some smaller than others; median space free, submedian space with curved CuP; curved cross-vein separates submedian and subdiscoidal spaces; subdiscoidal space posteriorly open and transverse, with 1A making sub-right angle in basal part. Discoidal cell free, closed basally, narrowly elongate, Rs and MA strongly separated at arculus; MA2 less than twice as long as basal side of discoidal cell; MA2 well aligned with distal free part of CuA. Distal free part of CuA dividing into CuA1 and CuA2; CuA2 curved, directed towards posterior margin. CuA1 relatively short, ending well basal of nodus level, with 12 posterior branches. CuA1 and MP well-separated, clearly parallel for a long distance, one row of intervening transverse cells. MP weakly curved, reaching posterior margin well distal of nodus; MA1 nearly straight, more or less parallel to MP, with one row of cells in basal part of postdiscoidal area, narrower than area between MP and CuA1. Possibly female based on shape of anal area.

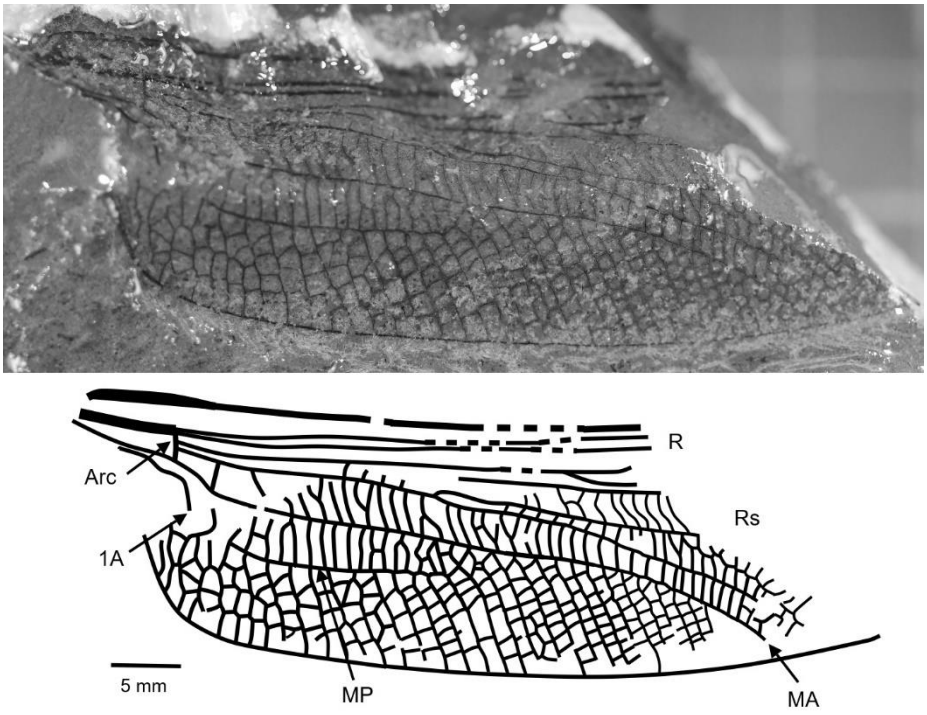

Figure 3.2. Holotype of *Lateophlebia anglicanopsis* (Zeuner, 1962) (NHMUK In.49573), modified from Kelly and Nel (2018b, fig. 2), Appendix 1.

Remarks.—L. anglicanopsis differs from the hindwings of Heterophlebiomorpha (including those of Liassophlebiidae) in the shape of the discoidal cell, which is narrowly elongate, with posterior side straight and distal side not twice as long as basal side. Also, there is no crossvein, complete or incomplete, in the discoidal cell. Furthermore, the shape of the cubito–anal area strongly differs from those in the Heterophlebiomorpha. 1A is not fused with CuA and the area between MP and CuA1 is broader than the postdiscoidal area. These characters are apomorphies of the Isophlebioidea. Thus, this species does not belong to the genus *Liassophlebia*. The species was originally attributed to the genus *Petrophlebia* (in the isophlebiomorphan family Architemistidae Tillyard, 1917). But it differs from *Petrophlebia* and the Architemistidae in the veins 1A and CuA2 being completely separated (Fig. 3.3).

Within the Isophlebioidea, *Lateophlebia* can be attributed to the Campterophlebiidae due to the opposite curvature of MA and MP constricting the area between them (apomorphy); basal part of area between MP and CuA1 less than twice as wide as basal part of area between MA1 and MP; distal side (MA2) of discoidal cell and gaff (basal CuA before its furcation) not orientated in one transverse axis.

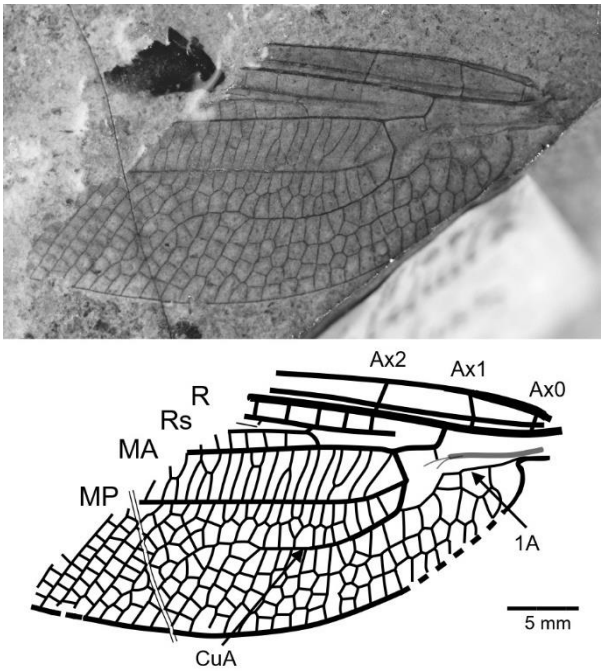

Figure 3.3. Holotype of *Petrophlebia anglicana* Tillyard, 1925 (NHMUK I.10494), modified from Kelly and Nel (2018b, fig. 3), Appendix 1.

Suborder ARCHIZYGOPTERA Handlirsch, 1906

Superfamily PROTOMYRMELEONTOIDEA Handlirsch, 1906

Family PROTOMYRMELEONTIDAE Handlirsch, 1906 Genus PROTOMYRMELEON Geinitz, 1887

Protomyrmeleon anglicanus Tillyard, 1925 *nomen dubium*

Holotype.—NHMUK I.10662 (Fig. 3.4) from Wainlode Cliff, Gloucestershire. upper Rhaetian (Penarth Group: Lilstock Formation: Cotham Member).

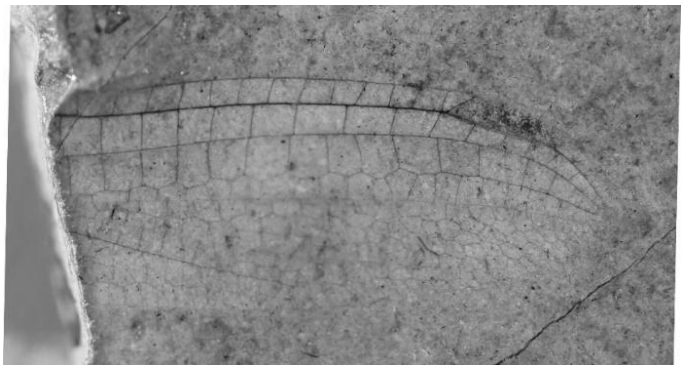

Figure 3.4. Holotype of *Protomyrmeleon anglicanus* Tillyard, 1925 (NHMUK I.10662) *nomen dubium*.

Remarks.—The holotype is only the apical third of a wing and so many of the main diagnostic characters are missing (Nel et al., 2005) so it is not possible to accurately identify this specimen, especially as it is the only known specimen for the species. This taxonomic change will be recorded in the literature in a future paper.

Family LIASSOPHLEBIIDAE Tillyard, 1925

Genus LIASSOPHLEBIA Tillyard, 1925

Type species.—*Liassophlebia magnifica* Tillyard, 1925

Emended diagnosis.—Cubito-anal area of hindwing large and broad, with 5–6 rows of cells between CuA and posterior wing margin; subdiscoidal space not divided into two large cells by an anterior branch of 1A that ends on CuA but divided into small cells; wings very large.

Liassophlebia magnifica Tillyard, 1925

1925 *Liassophlebia magnifica* Tillyard, p. 15, pl. 1, fig. 3 and pl. 2, fig. 4; text–figs 3–4.

1939 *Liassophlebia magnifica* Tillyard; Handlirsch, p. 23

1957 *Liassophlebia magnifica* Tillyard; Asahina, pp. 1–2, figs 1, 3.

1962 *Liassophlebia magnifica* Tillyard; Zeuner, p. 162, pl. 27, fig. 1.

1993 *Liassophlebia magnifica* Tillyard; Nel et al., p. 139, fig. 107.

1994 *Liassophlebia magnifica* Tillyard; Bechly, p. 16.

1995 *Liassophlebia magnifica* Tillyard; Trueman, p. 69.

2003 *Liassophlebia magnifica* Tillyard; Fleck et al., pp. 56, 86.

2003 *Liassophlebia magnifica* Tillyard; Rehn, p. 212.

Holotype.—NHMUK I.6648/I.10462 (Fig. 3.5), Planorbis Zone (Lias Group: Blue Lias Formation: Wilmcote Limestone Member); Early Jurassic: Lower Hettangian; Binton, Warwickshire.

Emended diagnosis.—Only hindwing characters known, anal branch forks into subdiscoidal space forming a distinct structure (also seen in *L. pseudomagnifica* but see below).

Remarks.—NHMUK I.11089 was also attributed to this species by Tillyard (1925) but only a partial abdomen is preserved so it is impossible to link it with any species described from wings. Also attributed to this species were: In.64000, In.59106 and In.49213 (Zeuner, 1962) but the first is the

holotype of *L. pseudomagnifica* Whalley, 1985; the second is the holotype of *Hypsothemis fraseri* Whalley, 1985 and the last is a fragment of the anterior margin of a wing and is not identifiable at this level. Possibly female based on shape of anal area.

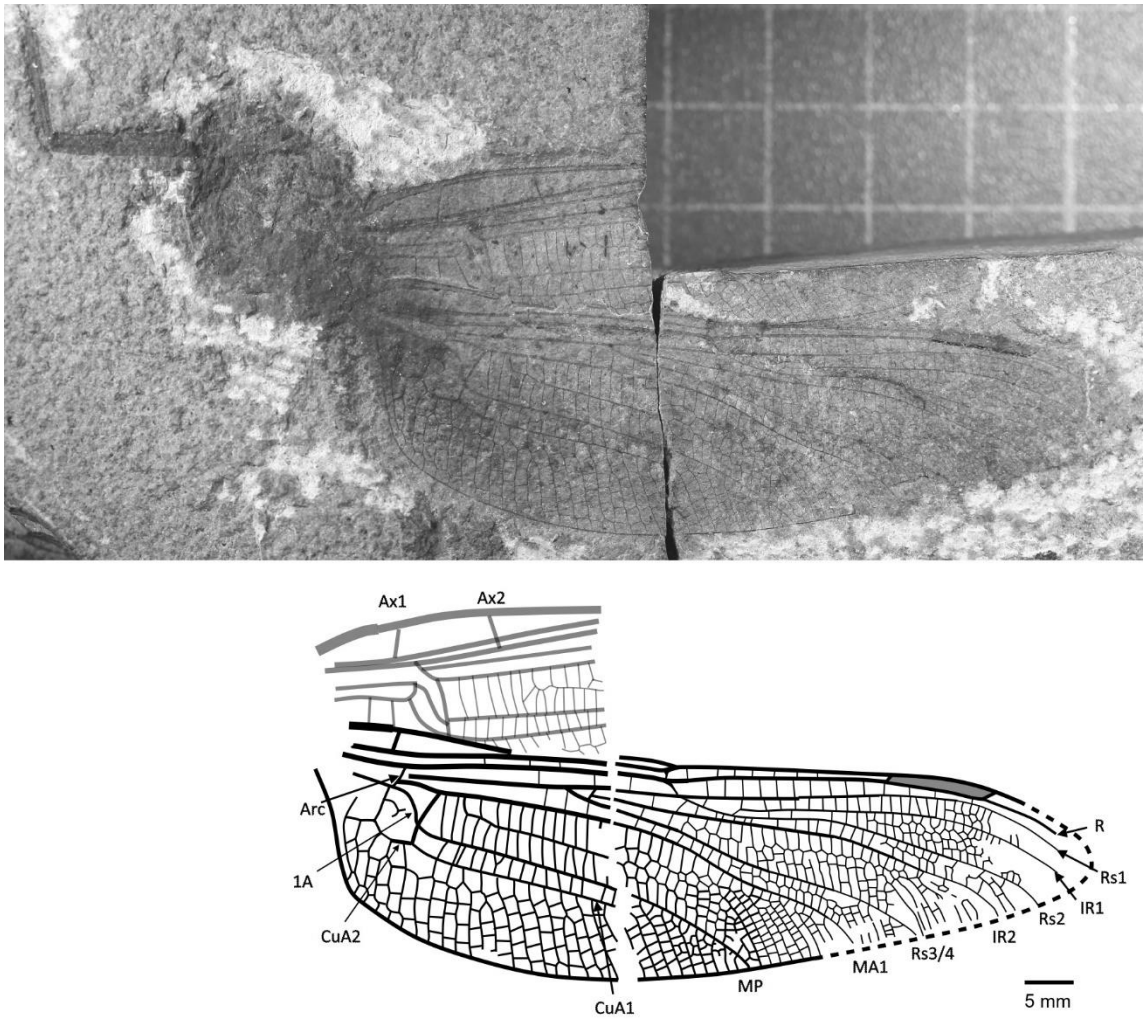

Figure 3.5. Holotype of *Liassophlebia magnifica* Tillyard, 1925 (NHMUK I.6648/I.10462), modified from Kelly and Nel (2018a, fig. 2), Appendix 2.

Liassophlebia withersi Tillyard, 1925

1925 *Liassophlebia withersi* Tillyard, p. 17, pl. 3, fig. 8.

1939 *Liassophlebia Withersi* Tillyard; Handlirsch, p. 23.

1962 *Liassophlebia withersi* Tillyard; Zeuner, p. 164.

1993 *Liassophlebia withersi* Tillyard; Nel et al., p. 142, fig. 106.

Holotype.—NHMUK I.10697 (Fig. 3.6), Insect Limestone/*Pseudomonotis* beds (Penarth Group: Lilstock Formation: Cotham Member); Late Triassic: upper Rhaetian; Strensham, Worcestershire.
Additional material.—NHMUK I.10528 from Strensham.

Diagnosis.—Similar to *L. magnifica* but smaller (distance from arculus to distal acute angle of discoidal cell 5.6 mm, against more than 6 mm in *L. magnifica*). Two anal cells, whereas three in *L. magnifica*.

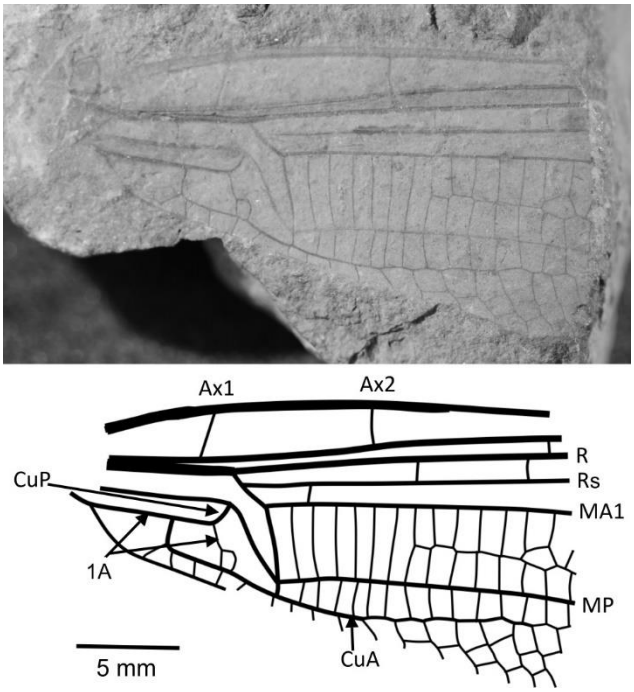

Figure 3.6. Holotype of *Liassophlebia withersi* Tillyard, 1925 (NHMUK I.10697), modified from Kelly and Nel (2018a, fig. 3), Appendix 2.

Remarks.—The two specimens discussed here are forewings whereas the other described species are known mostly from hindwings, except for the partial forewing in the holotype of *L. magnifica*. The differences between this partial forewing and the holotype of *L. withersi* are few and better-preserved specimens may lead to the synonymisation of this species with *L. magnifica*, or with one of the other species currently only described from hindwings. NHMUK I.10528 from the additional material is a forewing originally attributed to *L. batheri* (which is herein considered *nomen dubium*, see below). Upon examination, it is clear that there are few differences between this specimen and the holotype of *L. withersi* except for the aberration in the anal vein of the holotype I.10697 and an additional crossvein in the area immediately basal to the subdiscoidal cell. There is also a size difference, I.10697 is 10.1 mm in width when measured on level with the distal point of the discoidal triangle and I.10528 is 11.3 mm; the distance from the distal point of the discoidal triangle to the point at which the arculus meets the radial vein in I.10697 is 5.1 mm and in I.10528 is 6.4 mm. Upon further material being

described they may become different species but there is little justification to split them with the evidence available.

Liassophlebia pseudomagnifica Whalley, 1985

1962 *Liassophlebia magnifica* Tillyard; Zeuner, p. 162, pl. 27, fig. 1.

1985 *Liassophlebia pseudomagnifica* Tillyard; Whalley, p. 120, fig. 5a–b.

1993 *Liassophlebia pseudomagnifica* Tillyard; Nel et al., p. 139, figs 104–105.

2003 Liassophlebia pseudomagnifica Tillyard; Fleck et al., p. 56.

Holotype.—NHMUK In.64000, hw (Fig. 3.7), 'flatstones' (bed 83) of the Obtusum Zone: Obtusum Subzone (Lias Group: Charmouth Mudstone Formation: Black Ven Mudstone Member); Early Jurassic: Upper Sinemurian; Stonebarrow, Dorset.

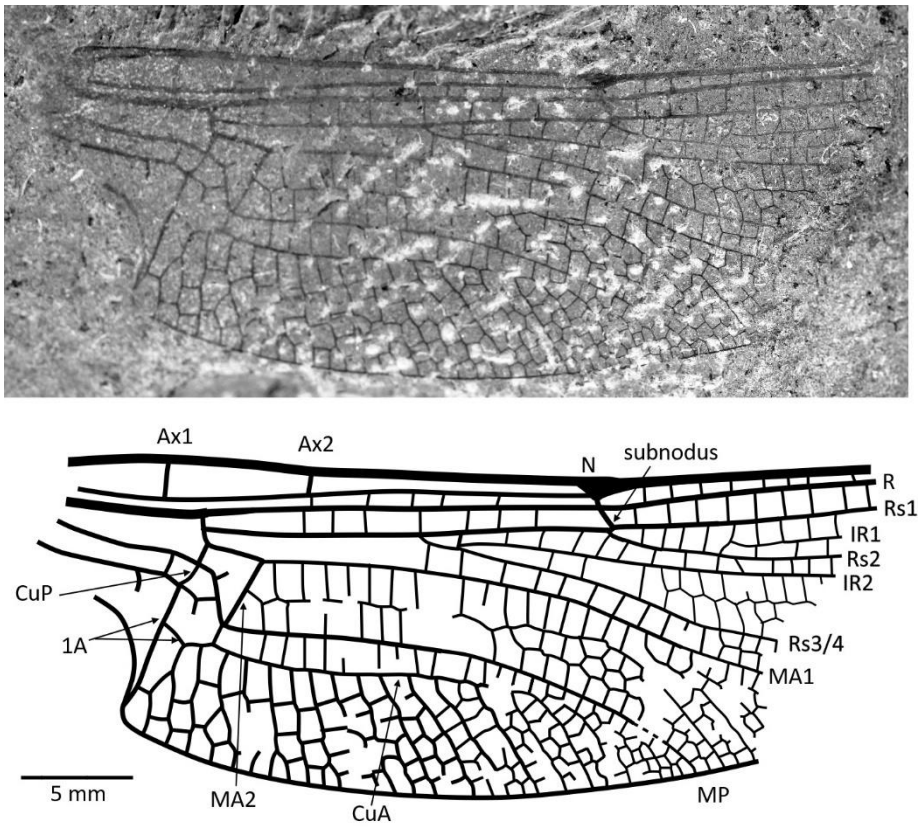

Figure 3.7. Holotype of *Liassophlebia pseudomagnifica* Whalley, 1985 (NHMUK In.64000), modified from Kelly and Nel (2018a, fig. 4) Appendix 2.

Diagnosis.—Hindwing: Anal branch forking into subdiscoidal space similar to that seen in *L. magnifica*; anal angle and triangle present.

Description.—See previous descriptions in Nel et al. (1993).

Remarks.—This species was split from *L. magnifica* based on a difference in the number of rows of cells between "M and Cu" by Whalley (1985) but it is clear from re–examination of the types that the number of rows is the same between the two specimens. Also, the peculiar shape of the anal vein in the subdiscoidal space is shared by both *L. magnifica* and *L. pseudomagnifica*, this shape is not seen in any other species of liassophlebid. The main differences between the two types of *L. magnifica* and *L. pseudomagnifica* concern the shape of the anal area and are related to sexual dimorphism (presence of an anal angle and triangle possibly suggests males), present in all Epiproctophora (= 'Anisozygoptera' + Anisoptera). Another difference concerns the supplementary longitudinal vein in basal part of postdiscoidal area that begins three cells distal of discoidal triangle in *L. magnifica* while it begins very close to it in *L. pseudomagnifica*. This difference could be due to intraspecific variation. There is no way to determine if they correspond to the same species until better preserved specimens are found.

Liassophlebia batheri Tillyard, 1925 *nomen dubium*

1925 *Liassophlebia batheri* Tillyard, p. 16, pl. 2, figs 5–6, pl. 3, fig. 7.

1939 *Liassophlebia batheri* Tillyard; Handlirsch, p. 23.

1993 *Liassophlebia batheri* Tillyard; Nel et al., p. 142.

Holotype.—NHMUK I.10434/10435 (Fig. 3.8), 'Insect Limestone' of the *Pseudomonotis* beds (Lilstock Formation: Cotham Member); upper Rhaetian; Strensham, Worcestershire.

Remarks.—The holotype for this species is at least a liassophlebiid based on comparison with the type species but there are very few other diagnostic characters preserved. Additionally, there are no comparable characters between this specimen and the forewing specimen Tillyard (1925) also named as a type (I.10528) so it is impossible to say whether they are the same species. I.10528 was found to be very similar to *Liassophlebia withersi* and has been attributed to this species herein. Compared to the type species of *Liassophlebia* (*L. magnifica*) the pterostigma of I.10434 is similar; there are less postnodal veins by 2–3 and several crossveins may be slightly more or less oblique leading to an assumption that they are similar. The diagnostic characters of *L. magnifica*, however, are not present and so it is impossible to accurately attribute this specimen to that, or other, species. Given the lack of diagnostic characters and the removal of the forewing from this type series it is clear that this species should be considered *nomen dubium*.

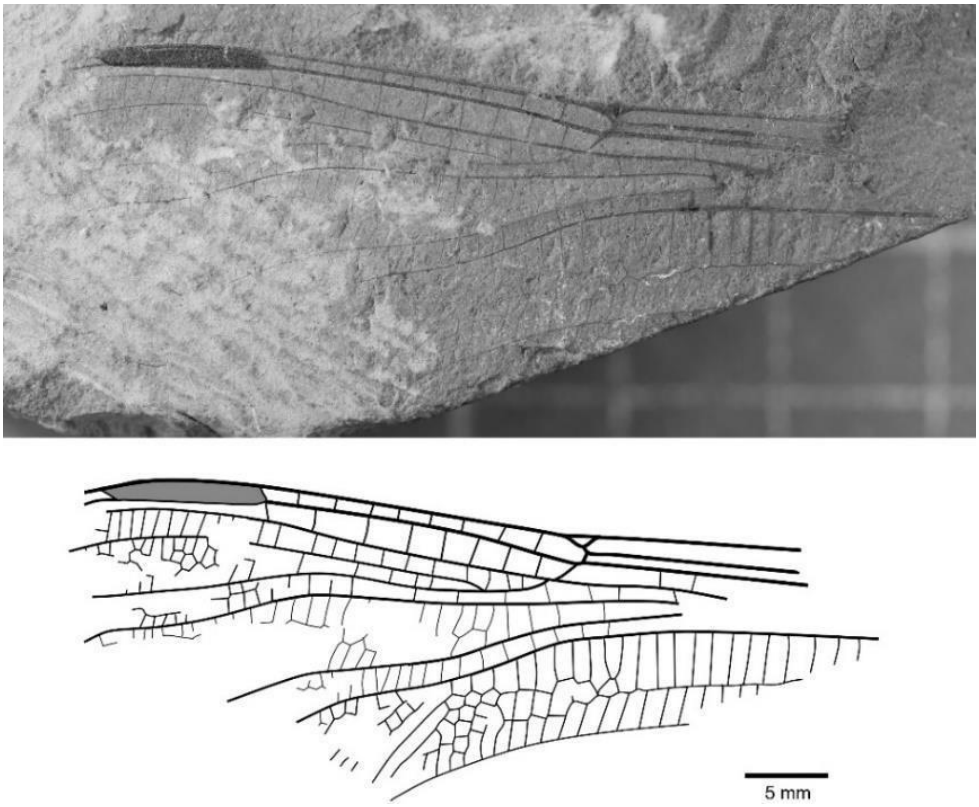

Figure 3.8. Holotype of *Liassophlebia batheri* Tillyard, 1925 *nomen dubium* (NHMUK I.10434/10435) from Kelly and Nel (2018a, fig. 5), Appendix 2.

Genus ROSSIPHLEBIA Kelly and Nel, (2018a)

lsid:zoobank.org:act:F69B2BC1-454C-46EF-B112-0599B2EF1AFF

Type species.—*Rossiphlebia jacksoni* (Zeuner, 1962).

Diagnosis.—Male hindwing characters known. Strong anterior branch of 1A ending on CuA and splitting subdiscoidal cell into two relatively large cells; cubital area wide (6–7 rows of cells); anal triangle split into two large cells, may suggest male; base of Rs2 aligned with subnodus. Well-defined supplementary longitudinal vein in basal part of postdiscoidal area, beginning very close to discoidal triangle (also present in *L. pseudomagnifica*).

Remarks.—This genus is very interesting as it seems to exhibit characters of both Liassophlebiidae and Heterophlebiidae. It is a liassophlebid due to the rudimentary discoidal triangle partly closed by an incomplete veinlet and the presence of a well-defined supplementary longitudinal vein in basal part of postdiscoidal area, but the division of the subdiscoidal cell is similar to the heterophlebiids, with a strong anterior branch of AA, but in male heterophlebiids the anal triangle is usually split into three

cells. The new genus is based on hindwing characters; thus, it is difficult to compare with *Ferganophlebia* and *Grimmenopteron* which are based only on forewings (Pritykina, 1970; Ansorge, 1996). Nevertheless, it differs from both of them in the presence of a well-defined supplementary longitudinal vein in basal part of postdiscoidal area. It is hardly comparable to *Bavarophlebia* which is based on a forewing only, but in the latter the base of Rs2 is distinctly distal of the subnodus while it is well aligned with it in *Rossiphlebia*.

Rossiphlebia jacksoni (Zeuner, 1962) 1962 *Liassophlebia jacksoni* Zeuner, p. 162, pl. 25, figs 1–2.

1985 *Liassophlebia jacksoni* Zeuner; Whalley, p. 121, fig. 6.

1993 *Liassophlebia jacksoni* Zeuner; Nel et al., p. 139, figs 102–103.

Holotype.—NHMUK In.53999 (pt and cpt) (Fig. 3.9), 'flatstones' (Bed 83) of the Obtusum Zone: Obtusum Subzone (Lias Group: Charmouth Mudstone Formation: Black Ven Mudstone Member); Early Jurassic: Upper Sinemurian; Stonebarrow, Dorset.

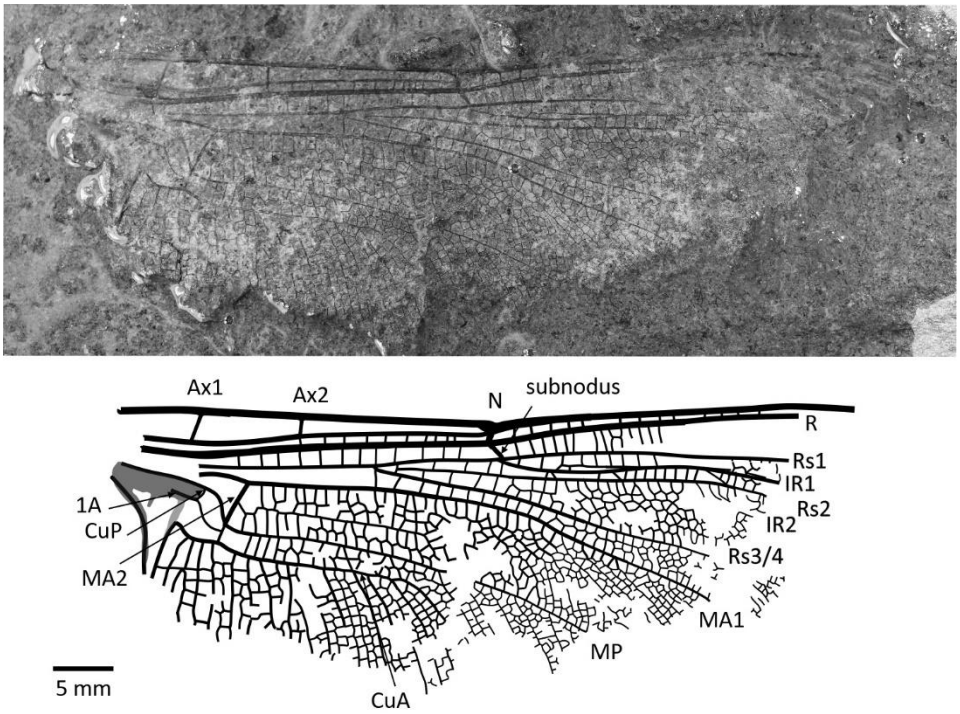

Figure 3.9. Holotype of *Rossiphlebia jacksoni (*Zeuner, 1962) (NHMUK In.53999), modified from Kelly and Nel (2018a, fig. 6), Appendix 2.

Additional material.—NMW 91.14G.1 Catherston Lane.

Diagnosis.—As for genus. Nine antenodal crossveins of second row; two–three rows of cells between MA1 and the supplementary longitudinal vein.

Family ANGLOPHLEBIIDAE Kelly and Nel (2018a)

lsid:zoobank.org:act:22C93C13-44F2-4292-BABC-5CB27D0B01E4

Type genus.—Anglophlebia Kelly and Nel, 2018a

Diagnosis.—Narrow wing with characters of both fore and hindwings of the Liassophlebiidae: 1A strongly curved posteriorly and straight (typical of forewings); posterior margin of subdiscoidal cell not convex and forking, with Cu appearing to head towards the posterior margin; subdiscoidal cell widened distally as in Liassophlebiidae; discoidal cell basally closed with shape reminiscent of liassophlebiid hindwings; subdiscoidal space divided into three or four cells; at least six cells between subdiscoidal cell and wing base; cubital area very narrow (forewing character); the intercalary vein begins at the first crossvein after the distal margin of the discoidal triangle (MA2) and is stronger and smoother than that of liassophlebiids; there are also more cells in the postdiscoidal area with a possible second posterior intercalary vein.

Remarks.—This is a peculiar specimen which seems to exhibit characters traditionally indicative of both fore– and hindwings. With the shape of the discoidal cell and the presence of the intercalary vein in postdiscoidal area, it could be identified as a hindwing, as indeed it was by Zeuner (1962). In the counterpart, however, the cubito-anal area is better preserved and exhibits characters of a forewing (1A curving strongly posteriorly; shape of anal area; narrow cubital area) and of a hindwing (discoidal cell basally closed; shape of discoidal cell; intercalary vein in postdiscoidal area; subdiscoidal cell divided). There are two possible hypotheses based on the evidence, firstly that we have a hindwing with a reduced cubito-anal area, as in some Campterophlebiidae (Nel et al., 2008) or that we have a forewing with some hindwing characters (as in the Liassogomphidae and modern Anisoptera in which the discoidal cell is divided into a hypertriangle and a discoidal triangle in the forewings, while in the Heterophlebiidae, this is only the case in the hindwings). Either way, and although the specimen is only the basal fragment, it is unique amongst the British material (checked at all known repositories of British Late Triassic/Early Jurassic material in the UK and the US), the Liassic material held at MNHN (checked by A. Nel), the Late Triassic/Early Jurassic Russian and Central Asian material (checked at PIN with Dmitry Vassilenko) and the Late Triassic/Early Jurassic material from China held at NIGPAS (examined by the senior author). The specimen does not fit with any family diagnosis already described and so we tentatively erect a new family for this species in the hopes that further better-

preserved specimens may be found and described in the future which lead to clearer understanding of the familial taxonomy of this specimen.

Genus ANGLOPHLEBIA Kelly and Nel (2018a)

urn:lsid:zoobank.org:act:4D1E9DF6-3627-4185-A445-760EFD8660DD

Type species.—Anglophlebia gigantea (Zeuner, 1962).

Diagnosis.—As for family.

Anglophlebia gigantea (Zeuner, 1962)

1962 *Liassophlebia gigantea* Zeuner, p. 163, pl. 27, fig. 2.

1985 *Liassophlebia gigantea* Zeuner; Whalley, p. 122, fig. 7a–b.

1993 *Liassophlebia gigantea* Zeuner; Nel et al., p. 139, fig. 108.

Holotype.—NHMUK In.51030 (pt and cpt) (fig. 3.10), 'flatstones' (Bed 83) of the Obtusum Zone: Obtusum Subzone (Lias Group: Charmouth Mudstone Formation: Black Ven Mudstone Member); Early Jurassic: Upper Sinemurian; Stonebarrow, Dorset.

Diagnosis.—As for genus.

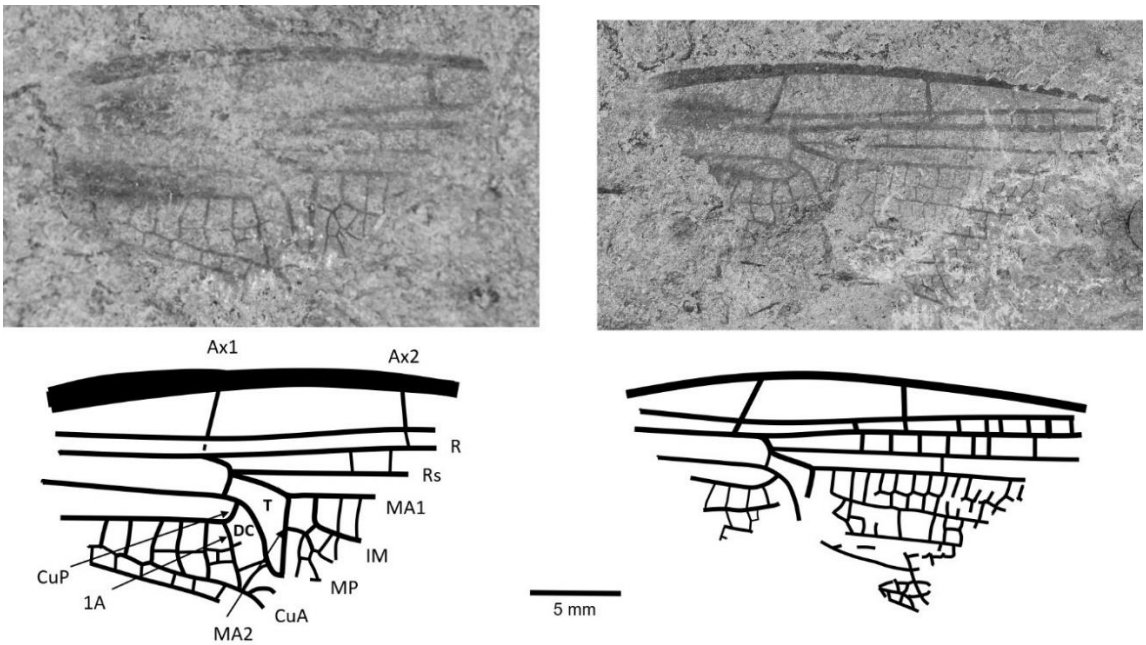

Figure 3.10. Holotype of *Anglophlebia gigantea* (Zeuner, 1962) (NHMUK In.51030), from Kelly and Nel (2018a, fig. 7), Appendix 2.

ODONATA incertae sedis

'Liassophlebia' clavigaster Tillyard, 1925

1925 *Liassophlebia* (?) *clavigaster* Tillyard, p. 19, pl. 3, fig. 9, text–fig. 5.

1939 (*Anisozygopteron*) *clavigaster* Tillyard; Handlirsch, p. 29.

1978 *Liassophlebia clavigaster* Tillyard; Lindley, p. 344.

1993 *Liassophlebia* (?) *clavigaster* Tillyard; Nel et al., p. 142, fig. 109.

Holotype.—NHMUK I.10433 (Fig. 3.11), 'Insect limestone' of the *Pseudomonotis* beds (Lilstock Formation: Cotham Member); Late Triassic: upper Rhaetian; Strensham, Worcestershire.

Figure 3.11. Holotype of *'Liassophlebia' clavigaster* Tillyard, 1925 (NHMUK I.10433), from Kelly and Nel (2018a, fig. 9), Appendix 2.

Remarks.—This specimen and the other identified as this species (NHMUK I.475) are known only from abdominal segments. Liassophlebiid higher taxonomy is based on wings so it is impossible to attribute this specimen to a genus or family. We therefore consider this species to be *incertae sedis* at all levels until such a time as a better-preserved specimen allows for identification. Stenophlebiidae have an apically widened abdomen similar to this one. Thus, it is not even possible to attribute this fossil to a precise group (Stenophlebiomorpha, Heterophlebioptera, etc.).

'*Liassophlebia' hopei* Tillyard, 1925

1845 *Libellula hopei* Brodie, pp. 71, 102, pl. 10, fig. 3.

1892 *Libellula hopei* Brodie; Woodward, p. 195.

1879 *Libellula hopei* Brodie; Goss p. 129.

1850 *Petalura liassina* (Strickland); Hagen, p. 359.

1850 *Heterophlebia hopei* (Brodie); Hagen, 1850, p. 359 (footnote).

1906 (*Anisozygopteron* ?) *hopei* (Brodie); Handlirsch, p. 470.

1939 (*Anisozygopteron*) *hopei* (Brodie); Handlirsch, p. 29.
1925 *Liassophlebia* (?) *hopei* (Brodie); Tillyard, p. 19.
1993 *Liassophlebia hopei* (Brodie); Nel et al., p. 143.

Holotype.—OUMNH J.55084 a&b (Fig. 3.12), 'Insect limestone' of the *Pseudomonotis* beds (Lilstock Formation: Cotham Member); Late Triassic: upper Rhaetian; Strensham, Worcestershire.

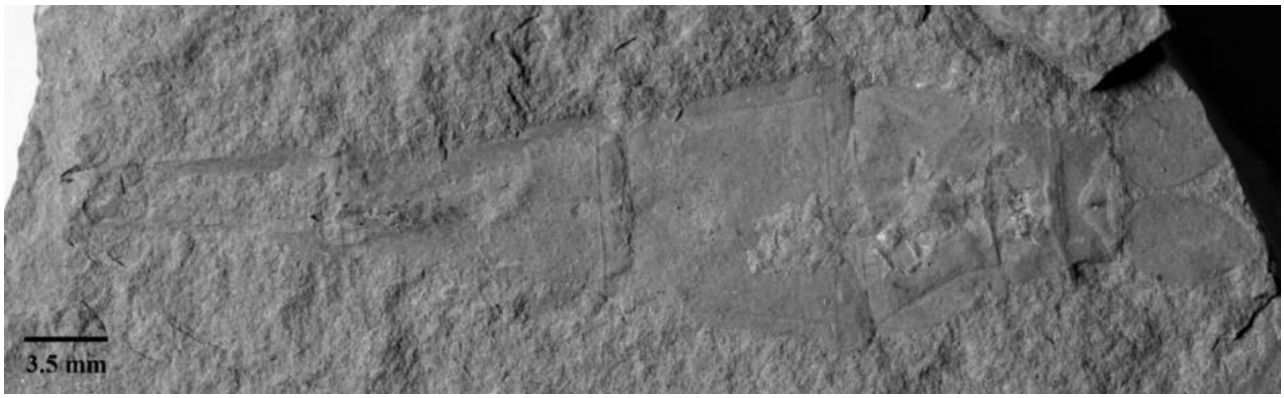

Figure 3.12. Holotype of *'Liassophlebia' hopei* Tillyard, 1925 (OUMNH J.55084), from Kelly and Nel (2018a, fig. 10), Appendix 2.

Remarks.—Same reasoning as for *clavigaster* above.

Conclusions.—*Lateophlebia* Kelly and Nel, 2018a was described in Campterophlebiidae for *Lateophlebia anglicanopsis* (Zeuner, 1962) which was redescribed. *Archithemis liassina* (Strickland, 1840) was transferred to this family. *Rossiphlebia* Kelly and Nel, 2018a. was described in Liassophlebiidae for *Liassophlebia jacksoni* Zeuner, 1962. *Liassophlebia gigantea* Zeuner, 1962 is unique in several key characteristics and so was transferred to *Anglophlebia* Kelly and Nel, 2018a in Anglophlebiidae Kelly and Nel, 2018a. *Liassophlebia batheri* Tillyard, 1925 was considered *nomen dubium. Protomyrmeleon anglicanus* Tillyard, 1925 was considered *nomen dubium*.

3.3.2 Dermaptera

This order contains the earwigs, very distinctive insects (Fig. 3.13) with truncated leathery forewings (also known as tegmina, often the only part to preserve) and an elongate, dorsoventrally flattened body with cerci that are modified into forceps in the younger taxa (Gullan and Cranston, 2010). The pronotum is rectangular with rounded edges, and the head is triangular and prognathous with well-developed compound eyes. Hindwing morphology is unique to this order, with an extensive anal region, reduced remigium, and unique folding mechanism (Grimaldi and Engel, 2005). There are

few instances, however, of hindwings in the fossil record, most earwig fossils from the Mesozoic are known from isolated tegmina (Kelly et al., 2018b). Some of the earliest known earwigs were collected from the Late Triassic of the UK (Jarzembowski, 1999), although they were not described in detail prior to this project (Kelly et al., 2018b). Previously these specimens have been considered as hemipterans (Brodie, 1845), orthopterans (Giebel, 1856), or coleopterans (Cockerell, 1915). Three earwig species have been described from the Early Jurassic, namely, *Brevicula gradus* Whalley, 1985 (Charmouth Mudstone Formation, Sinemurian, of England), *Baseopsis forficulina* Heer, 1865 (Staffeleg Formation, Hettangian, Switzerland), and *B. sibirica* Brauer et al., 1889 (Toarcian of Russia). The latter species is based on a fragmentary larval specimen which cannot be located for reexamination.

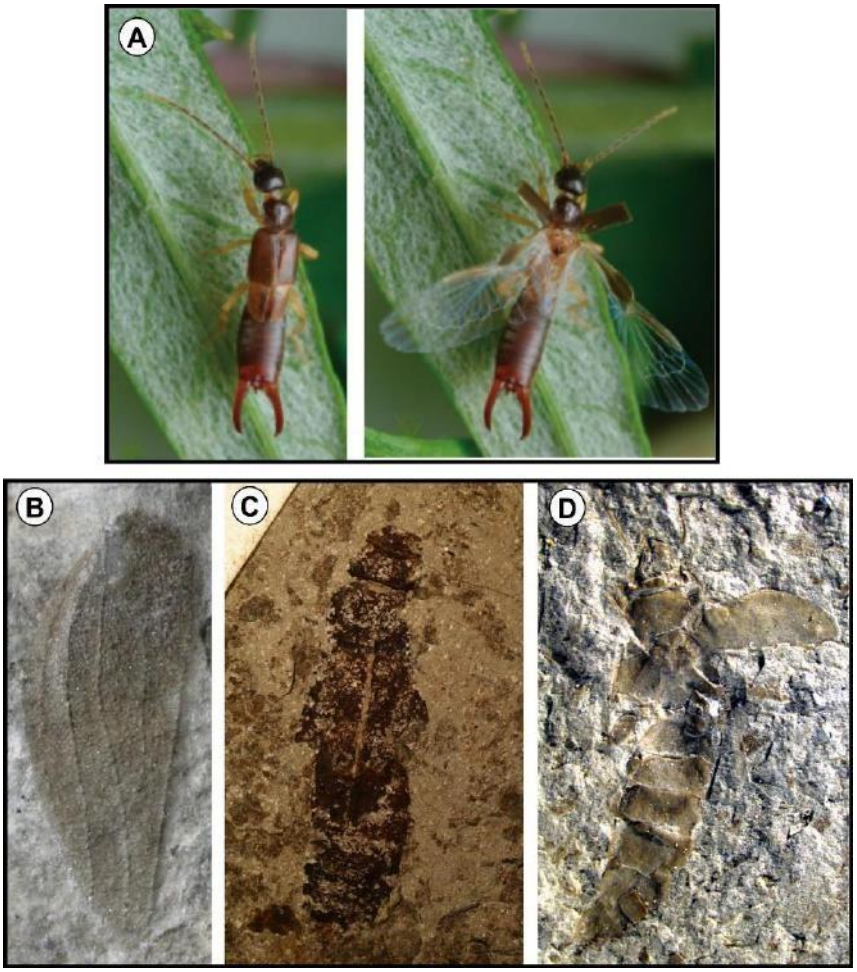

Figure 3.13. Some examples of earwigs of the order Dermaptera. A. Extant earwig, *Labia minor* (photo from Kim and Nishikawa, 2017), B. Triassic earwig, *Phanerogramma heeri* (NHMUK I.10943), C. Jurassic earwig, *Baseopsis forficulina* (Heer collection, ETH), D. Jurassic earwig from China (Xinjiang collection, NIGPAS).

Systematic Palaeontology

Order DERMAPTERA de Geer, 1778
Suborder ARCHIDERMAPTERA Bei-Bienko, 1936
Superfamily PROTODIPLATYOIDEA Martynov, 1925
Family ?DERMAPTERIDAE Vishniakova, 1980

Type genus.—Dermapteron Martynov, 1925 nom. transl. Vishniakova, 1980

Remarks.—The family Dermapteridae was originally named as the subfamily Dermapterinae Vishniakova, 1980 and was later elevated to family status without discussion (Engel, 2003). Sinopalaeodermatidae Zhang, 2002 was included as a junior synonym (Engel and Haas, 2007). The subfamily name was Latinised based on *Dermatopteron* Martynov, 1925, originally proposed as a collective group. The Greek spelling was later restored (Nel et al., 2012), but as this is an unnecessary change, we have followed Vishniakova. The question mark in 'Family ?Dermapteridae Vishniakova 1980' above is to denote uncertainty as to the placement of the genera described below, not to question the authority of the family name.

Genus PHANEROGRAMMA Cockerell, 1915

Emended Diagnosis.—Tegmina not truncated, tuberculate, with evenly curved anterior margin. M and Cu have a common origin, Cu simple.

Type species.—Phanerogramma heeri (Giebel, 1856)

Remarks.—Brodie (1845, pl. 8, figs 15, 17, 18) figured three specimens from the 'Lower Lias' of England and considered them to 'either be the hemtegmen of some new genus of Homoptera, or some curiously striated tegmen of a beetle' (Brodie, 1845, p. 128). Giebel (1856) named two of Brodie's figured specimens as two new species of the extant orthopteran genus *Akicera*: *A. heeri* and *A. frauenfeldi*. In Brodie (1845, p. 101) a mistake led to one of the figures (fig. 17) being listed as 'Blattidae?' from Wainlode and Strensham; however, this should probably have been a reference to figure 13 instead, which is a partial blattodean (cockroach) wing. This led to (Scudder, 1891, p. 104) incorrectly citing *A. heeri* as being from these localities. Cockerell (1915) synonymized the two species and placed them in the new genus *Phanerogramma* in the beetle (Coleoptera) family Tenebrionidae where the taxon has languished ever since. *P. heeri* became the senior synonym over *P. frauenfeldi*.

Of the three specimens figured by Brodie, two are clearly labelled; however, the third cannot be found. Unfortunately, the missing specimen is the holotype of *Phanerogramma heeri*. A thorough search through the 19 Dermaptera tegmina in the Brodie collection at the NHMUK has not established if any one of them could be the missing type. They came from several different localities but unfortunately the location of the type is not known. Either this specimen is present but unlabelled and impossible to recognise or it is missing. For this reason, a neotype is required for *Phanerogramma heeri* from Brodie's collection.

All the tegmina are characteristic in having a distinctive tuberculate ornament. *Dermapteron incertus* (nom. correct pro *incerta* Martynov, 1925) (Dermapteridae) and *Asiodiplatys speciosus* Vishniakova, 1980 (Protodiplatyidae) both have a granular ornament within the Protodiplatyoidea; however, *Dermapteron* has a richer venation (see Vishniakova, 1980). *Phanerogramma* is also similar to *Sinopalaeodermata neimonggolensis* Zhang, 2002 and *Palaeodermapteron dicranum* Zhao et al., 2011, both within the Dermapteridae (*sensu* Engel and Haas, 2007). *Phanerogramma* differs from *Dermapteron*, *Sinopalaeodermata* and *Palaeodermapteron* in having a more evenly curved anterior margin and Cu is simple not forked. *Phanerogramma* certainly belongs to the Protodiplatyoidea but given that the body morphology is not known it is only tentatively placed within the family Dermapteridae based on the venation.

Phanerogramma heeri (Giebel, 1856)

1845 Hemelytra of Homoptera or beetle Brodie; p. 128, pl. 8, figs 17, 18.
1856 *Akicera heeri* Giebel, p. 310.
1856 *Akicera frauenfeldi* Giebel, p. 310.
1879 *Akicera heeri* Giebel; Goss, p. 146.
1879 *Akicera frauenfeldi* Giebel; Goss, p. 146.
1891 *Akicera frauenfeldi* Giebel; Scudder, p. 104 (no. 611).
1891 *Akicera heeri* Giebel; Scudder; p. 104 (no. 612).
1906 (?Locustidae) *heeri* Giebel; Handlirsch, p. 423.
1906 (?Locustidae) *frauenfeldi* Giebel; Handlirsch, p. 423.
1915 *Phanerogramma heeri* (Giebel); Cockerell, p. 479, pl. 60, fig. 10.
1992 *Phanerogramma heeri* (Giebel); Carpenter, p. 324.
1999 Unnamed dermapteran Jarzembowski, p. 150–1, fig. 12B.

Neotype.—NHMUK I.10961 (Fig. 3.14), Brodie coll., '*Pseudomonotis* beds' (Penarth Group: Lilstock Formation); Late Triassic: upper Rhaetian; Forthampton, Gloucestershire. Figd. Jarzembowski (1999).

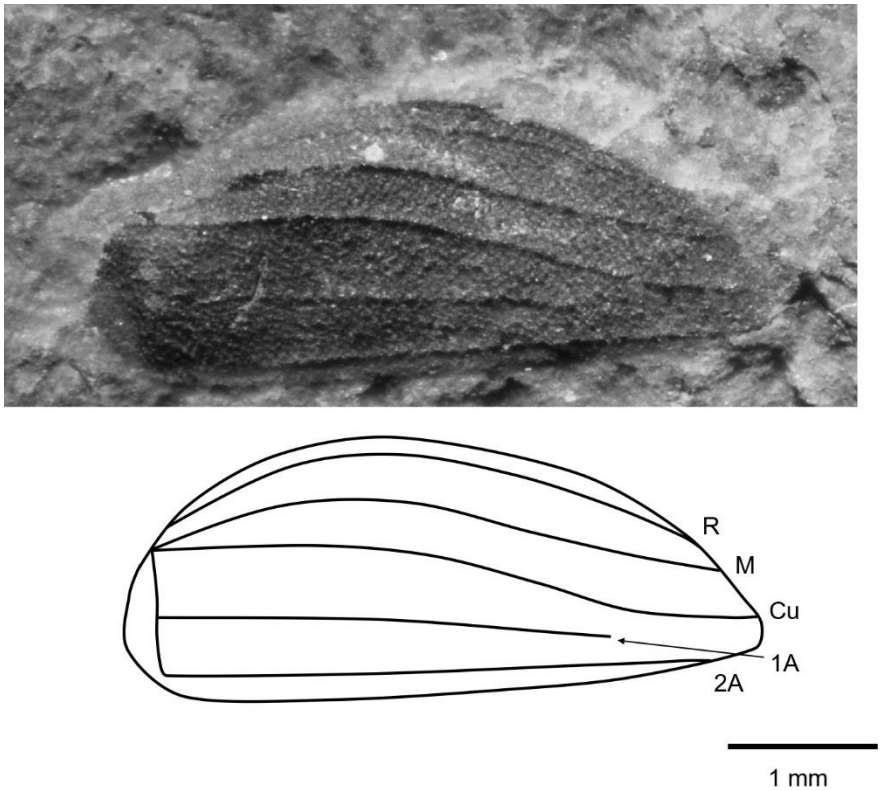

Figure 3.14. Neotype of *Phanerogramma heeri* (Giebel, 1856) (NHMUK I.10961), from Kelly et al. (2018b, fig. 5), Appendix 3.

Additional material.—Rhaetian: NHMUK I.10943, I.11254 Apperley; USNM 61405 (Lacoe 3452, figured by Cockerell, 1915), NHMUK I.10619, I.10870, I.10985 Brown's Wood; I.11559 Forthampton; I.11002, I.11004 Norton; I.3569 (Holotype of *P. frauenfeldi*), I.10978, I.10981, II.1946 Wainlode. Hettangian: NHMUK I.11020 Copt Heath. Unknown: OUMNH J.55104, MCZ PALE 8667 locality unknown.

Emended diagnosis.—Tegminal length 4.6–6.0 mm, width 1.7–2.3 mm. Evenly pigmented; R running close to C; M and Cu terminate at wing–tip; Cu, 1A and 2A equidistant at base, 2A straight.

Description.—Tegmina not truncated, tuberculate, pigmented, with curved anterior margin and straight posterior margin. R faint and simple, runs parallel and close to C, terminating on C just before the tip; M simple, forms a keel at the base, gently curved then straightens out, terminates at tip; Cu simple, originating at same point as M, initially diverges from M then runs parallel to it, converging towards 2A and terminates at tip; A apparently running straight posteriorly with simple 1A branching half–way and fades out, 2A simple, runs parallel to posterior margin and terminates at tip.

Remarks.—The figure in Jarzembowski (1999) of the neotype (I.10961) is upside down and has been turned the right way up here resulting in false relief. Cockerell's figure of USNM 61405 appears to show an emarginated tegmen, however, part of the tegmen is missing at that point. The specimens certainly occur in rocks of Rhaetian and Hettangian age and there is nothing to distinguish between them, thus this species crosses the Tr/J boundary.

Phanerogramma gouldsbroughi Kelly et al., 2018b

LSID: urn:lsid:zoobank.org:act:4DB85CD0-2217-4DFE-BC63-8A9C5805395F

1845 Hemelytra of Homoptera or beetle Brodie, p. 128, pl. 8, fig. 15.

1906 (*Coleopteron*) sp. Handlirsch, p. 457, pl. 41, fig. 75.

Holotype.—NHMUK I.3578 (Fig. 3.15), Brodie coll., Rhaetian or Hettangian; 'near Bristol' (exact locality and age not known).

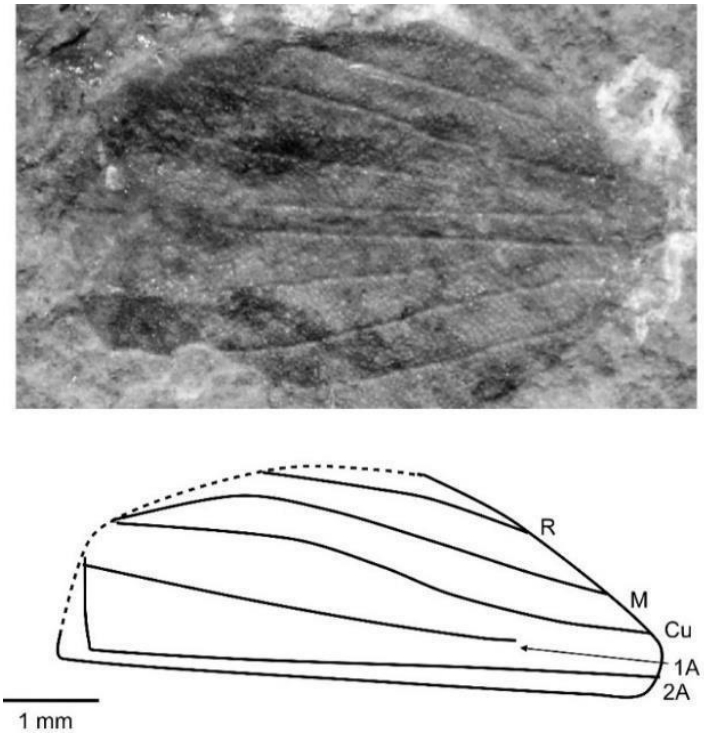

Figure 3.15. Holotype of *Phanerogramma gouldsbroughi* Kelly et al., 2018b (NHMUK I.3578), from Kelly et al. (2018b, fig. 6), Appendix 3.

Diagnosis.—Tegminal length 6.8 mm, width 2.8 mm. Differs from *P. heeri* and other species in that it is significantly larger, and it appears to have a colour pattern. M terminates just before the tip.

Description.—Paired tegmina not truncated, tuberculate, pigment pattern, with curved anterior margin and straight posterior margin. R simple, very faint either missing from the left tegmen or mostly obscured on the right; M simple, gently curved then straightens out, terminates just before tip; Cu simple, nearly straight, runs parallel to M, converging towards 2A and terminates at tip; origination of A not visible but assumed to be similar to *P. heeri*; simple 1A merges with 2A on left tegmen, but fades out on right tegmen, thus demonstrating variation; 2A simple, runs parallel to posterior margin and terminates at tip.

Family PROTODIPLATYIDAE Martynov, 1925

Genus BREVICULA Whalley, 1985

Type species.—Brevicula gradus Whalley, 1985.

Emended diagnosis.—Punctate tegmina without venation, reaching third abdominal segment. Posterior margin straight to slightly convex and the anterior margin emarginate. Coxae short, rounded. Ovipositor present in females.

Brevicula gradus Whalley, 1985

Holotype.—NHMUK In.53993 (Fig. 3.16), female with ovipositor, Jackson coll., ‘flatstones’ (Bed 83) of the Obtusum Zone: Obtusum Subzone (Lias Group: Charmouth Mudstone Formation: Black Ven Mudstone Member); Early Jurassic: Upper Sinemurian; Black Ven, Dorset.

Paratype. NHMUK In.51036, Jackson coll. Females with ovipositor from ‘woodstones’ (Bed 83) of the Obtusum Zone: Obtusum Subzone (Lias Group: Charmouth Mudstone Formation: Black Ven Mudstone Member); Early Jurassic: Upper Sinemurian; Black Ven, Dorset.

Additional material.—II.2181 Sole coll. Female with ovipositor from woodstones of Black Ven. II 3087, II 3088 both Coram coll., Monmouth Beach (all Sinemurian).

Emended diagnosis.—As for genus, with tegminal posterior margin straight.

Description.—(emended from Whalley, 1985). Length (tip of head to tip of ovipositor) 10–12 mm, width of abdomen 2–2.2 mm. Head prognathous; only base of filiform antennae preserved; prothorax rounded; tegmina strongly punctate, elongate; probably reaching third abdominal segment; abdomen

parallel sided, with at least six visible segments, terminal segment rounded; legs cursorial, slender, femora slightly thickened, tibia thin, 4 or 5 segmented tarsi. Pointed ovipositor in females. Cerci not visible, probably not preserved, which may indicate they were fine and filiform.

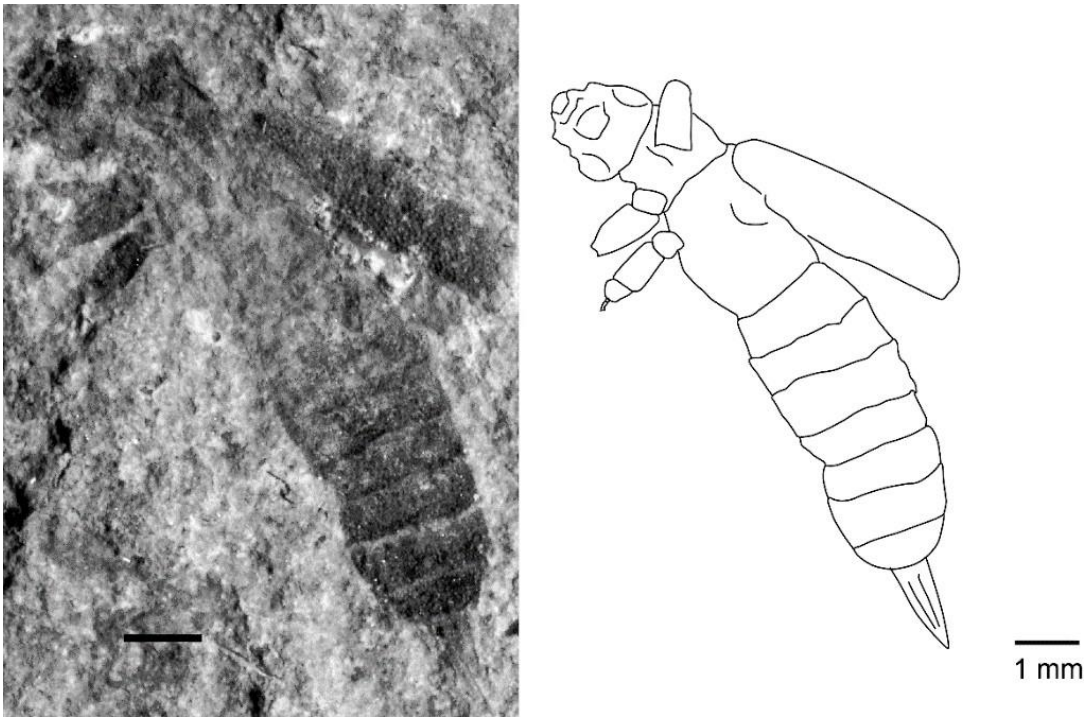

Figure 3.16. Holotype of *Brevicula gradus* Whalley, 1985 (NHMUK In.53993), from Kelly et al. (2018b, fig. 11), Appendix 3.

Remarks.—This taxon was originally considered to possess two slender forceps (Whalley, 1985) however, this structure does not appear to be divided and is much more likely to be an ovipositor (Nel et al., 2012). Although originally described as a dermapteran, Zhang (2002) considered that this taxon should 'bear more primitive features' than other fossil Dermaptera and considered it could be a beetle in the family Staphylinidae instead, which are similar morphologically to earwigs. The presence of the ovipositor of *B. gradus* indicates it is certainly a dermapteran. The presence of older Dermaptera (*Phanerogramma*) indicates that they had certainly appeared by the Late Triassic and more derived forms with no venation could have evolved by the Sinemurian. The presence of the ovipositor and absence of distinct forceps indicates that this taxon probably only had primitive, simple, filiform cerci (not preserved) typical of the family Protodiplatyidae, such as in *Longicerciata mesozoica* Zhang, 1994 and *Sinoprotodiplatys zhangi* Nel et al., 2012.

Brevicula maculata Kelly et al., 2018b

LSID: urn:lsid:zoobank.org:act:10B077EF-BF86-4AE6-9B77-42ADD4910C62

Holotype.—NHMUK II 3086 (Fig. 3.17) Coram coll., Turneri Zone (Lias Group: Charmouth Mudstone Formation: Black Ven Mudstone Member); Early Jurassic: Lower Sinemurian; Monmouth Beach, Dorset.

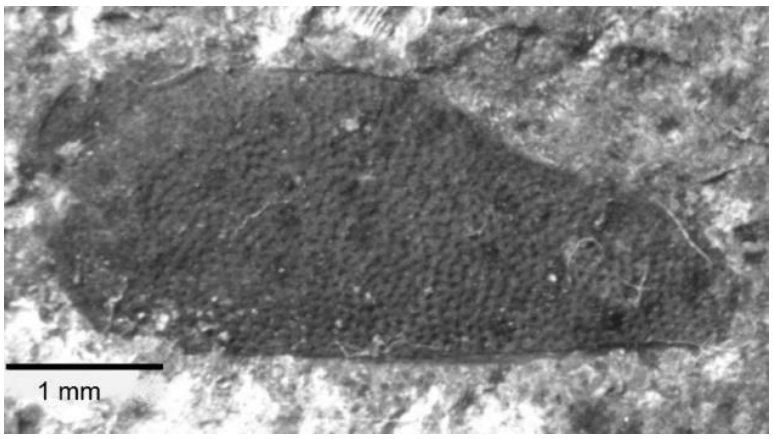

Figure 3.17. Holotype of *Brevicula maculata* Kelly et al., 2018b (NHMUK II 3086), from Kelly et al. (2018b, fig. 12), Appendix 3.

Diagnosis.—Tegmina as for genus with slightly convex posterior margin. Anterior margin straight for just over half of tegminal length then sigmoidally curved to blunt apex. Venation absent; distinct spots present.

Description.—Isolated tegmen, length 4.5 mm, width 1.5 mm. Many dark spots visible over tegminal surface.

Remarks.—Holotype donated to the NHM by Rob Coram for the purpose of this study. This is the only known fossil earwig specimen with spots.

DERMAPTERA incertae sedis

Remarks.— There is one more isolated tegmen known from the Mesozoic of England. It consists of a faint impression but certainly appears to be different from other fossil taxa; however, in the absence of more distinct characters, it cannot be placed in any family.

Genus TRIVENAPTERON Kelly et al., 2018b

LSID: urn:lsid:zoobank.org:act:BC9E587B-73B5-4AC2-BE70-AACF9003DFB2

Type species.—*Trivenapteron moorei* Kelly et al., 2018b

Diagnosis.—Differs from other fossil dermapteran tegmina in that it has three prominent, diverging veins– probably R, M and Cu, plus a simple A vein.

Remarks.—This genus is also present in the Lower Toarcian Posidonia Shale Formation of Germany (Ansorge coll., personal observation), with several probable new species that are to be described in an upcoming paper.

Trivenapteron moorei Kelly et al., 2018b

LSID: urn:lsid:zoobank.org:act:9711F5FD-AE27-46A0-ACB1-96266F9CEE31

2015 Earwig tegmen Williams et al., p. 686.

Holotype.—TTNCM 489 (Fig. 3.18) Moore coll., 'Fish and insect beds' of the Falciferum Zone (Lias Group: Beacon Limestone Formation); Early Jurassic: Lower Toarcian; Strawberry Bank, Ilminster, Somerset.

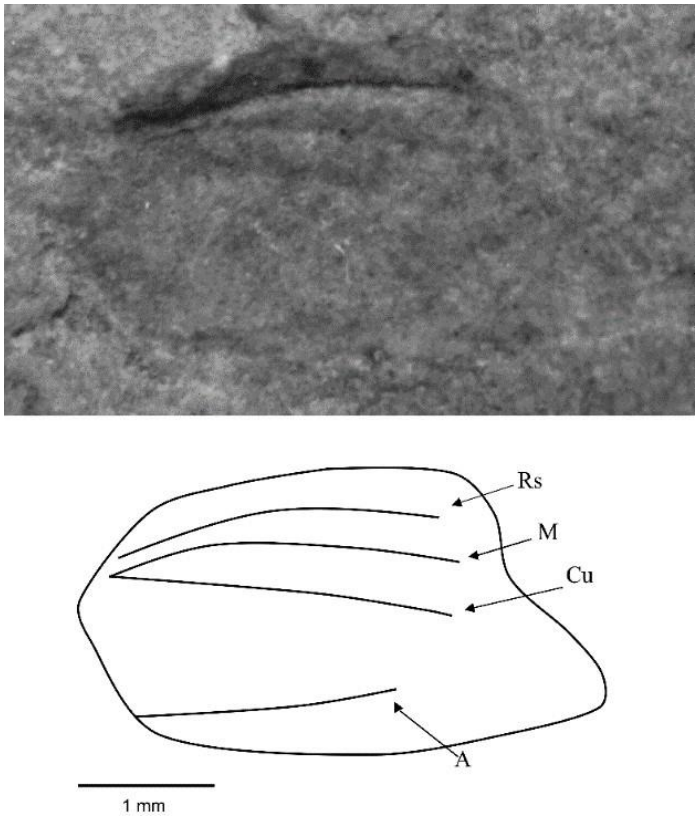

Figure 3.18. Holotype of *Trivenapteron moorei* Kelly et al., 2018b (TTNCM 489), from Kelly et al. (2018b, fig. 14), Appendix 3.

Diagnosis.—As for genus; monotypic.

Description.—Tegminal length 3.9 mm, tegminal width 2.3 mm. Sub-quadrate, truncate tegmen, pointed apically and without ornament. Three diverging veins with M and Cu having a common origin, plus a simple A vein running near to the posterior margin.

Conclusions.—*Phanerogramma heeri* (Giebel, 1856) was transferred from the Coleoptera (beetles) to the Dermaptera (earwigs) and was redescribed, as was *Brevicula gradus* Whalley, 1985. Three new species were described: *Phanerogramma gouldsbroughi* Kelly et al., 2018b, *Brevicula maculata* Kelly et al., 2018b, and *Trivenapteron moorei* Kelly et al., 2018b (including the new genus). *Phanerogramma* was tentatively considered in Dermapteridae.

3.3.3 Orthoptera

This order contains the crickets, grasshoppers, katydids and allies, at least the first two of which are relatively abundant and diverse in the Late Triassic and Early Jurassic of England with six families recorded: Bintoniellidae Handlirsch, 1939, Elcanidae Handlirsch, 1906, Haglidae Handlirsch, 1906, Protogryllidae Zeuner, 1937, Regiatidae Gorochov, 1995 and Locustopseidae Handlirsch, 1906. The first five of these are crickets ('long-horned grasshoppers') in the suborder Ensifera (Fig. 3.19), Locustopseidae is the only known family in the suborder Caelifera ('short-horned grasshoppers') (Fig. 3.20). Crickets are characterised by long antennae (over 30 segments), sword-shaped ovipositor and wings with stridulatory apparatus whereas grasshoppers have short antenna and wings lacking stridulatory apparatus (they make sound with their legs) (Grimaldi and Engel, 2005; Gullan and Cranston, 2010). Some primitive ensiferan wings also lack stridulatory apparatus and can appear superficially similar to caeliferan wings (e.g. Elcanidae and Bintoniellidae, see descriptions below), except for the basal fusion of the posterior medial and anterior cubital veins, a synapomorphy of caeliferans (Grimaldi and Engel, 2005).

Bintoniellidae was erected for the species *Bintoniella brodiei* Handlirsch, 1939 which was originally figured as a specimen of '*Chauliodes*' in Brodie (1845, pl. 10, fig. 9). The genus name refers to the prolific Hettangian locality of Binton in Warwickshire where the holotype was collected. Additional Kyrgyz taxa have been described (Sharov, 1968; Gorochov, 1987, 1989, 1994); and the family was transferred to Oedischioidea (Sharov, 1968) and then the genus to the subfamily Bintoniellinae (Gorochov, 1987). *B. brodiei* was subsequently re-described (Whalley, 1982; Béthoux, 2012). *B. brodiei* was the only recognised species until the current study in which it was found that there are actually two species present.

The family Haglidae refers to ambidextrous or hump-winged crickets which were much more abundant and diverse in the Mesozoic entomofaunas (Rasnitsyn and Quicke, 2002). All species are ground dwelling and live in coniferous forests where they ascend tree boles after dark to broadcast their songs (Resh and Cardé, 2009). The family has been previously considered as a synonym of Prophalangopsidae (Zeuner, 1935, 1939) with species described as prophalangopsids even though Haglidae had date priority. These families were formally split by with the extant taxa in Prophalangopsidae (Gorochov, 1995).

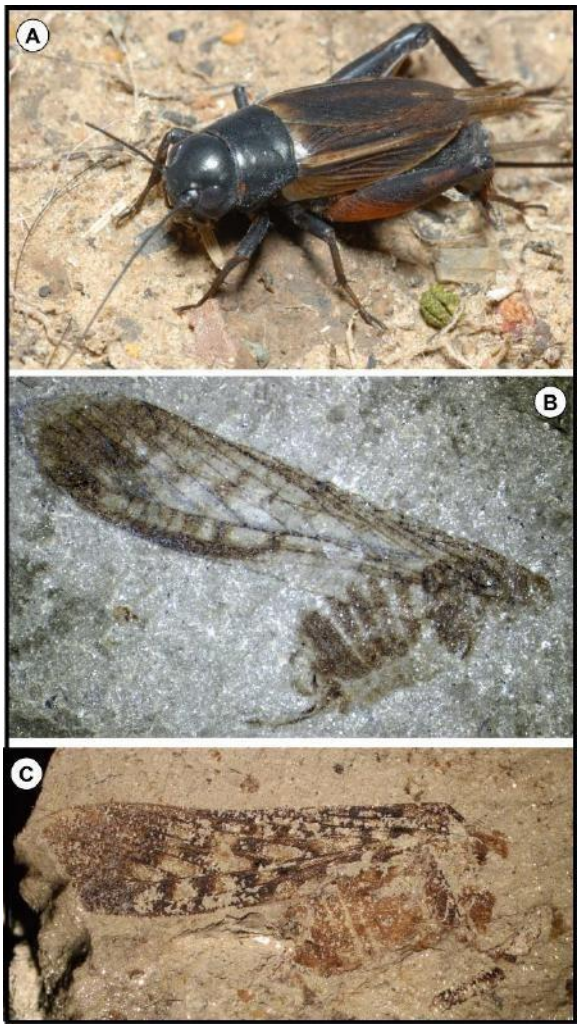

Figure 3.19. Examples of crickets of the suborder Orthoptera: Ensifera. A. Extant cricket, Gryllidae: *Gryllus* (photo by Blake Layton), B. Jurassic cricket, *Archelcana liasina* (NHMUK I.6702), C. Jurassic cricket, *Archelcana sp.* (Heer collection, ETH).

Hagla gracilis Giebel, 1856 was named from another of Brodie's '*Chauliodes*' specimens (Brodie, 1845, pl. 8, fig. 14) as was *H. similis* Giebel, 1856 (Brodie, 1845, pl. 8, fig. 6) and *H. deleta* Giebel, 1856 (Brodie, 1845, pl. 8, fig. 3). *H. anglica* Handlirsch, 1906 was named after another Brodie specimen (Brodie, 1845, pl. 10, fig. 5). *Liassophyllum* was erected for *L. abbreviatum* Zeuner, 1935 in the

subfamily Cyrtophylltinae, from the Hettangian of Binton (Slatter collection). *Protohagla* was then erected for *P. langi* Zeuner, 1962 from the Sinemurian of Dorset. *H. similis* and *H. deleta* were synonymised with *H. gracilis* (Wappler, 2001).

The family Elcanidae was erected by Handlirsch (1906) for the genus *Elcana* Giebel, 1856 which was originally placed in the family Panorpidae (Mecoptera). Handlirsch also described 32 new species from Germany and transferred several species to the family including *Rapha liasina* Giebel 1856 which was originally figured as '*Ephemera'* by Brodie (1845). *E. liasina* Cockerell, 1915 was described from the Lacoe collection of British material held in the US (Cockerell, 1915) but Handlirsch (1939) renamed these specimens as the new species *E. cockerelli* Handlirsch, 1939.

Archelcana Sharov, 1968 was erected for *A. shurabica* Sharov, 1968 from Kyrgyzstan and *A. britannica* (Handlirsch 1906). *A. durnovaria* Whalley, 1985 was added to the genus from the Jurassic Coast of Dorset (Whalley, 1985). The subfamilies Elcaninae Handlirsch, 1906 and Baisselcaninae Sharov, 1968 were later erected (Gorochov, 1986). The family was revised, and many species were synonymized (Zessin, 1987), as were the genera *Archelcana* and *Elcana*, the latter being the senior synonym. Whalley (1985) and the British material was not considered in this revision. *Elcana* and *Baisselcana* were then also synonymised with *Panorpidium* (Jarzembowski, 1996).

Due to the synonymisation of *Panorpidium* with *Baisselcana*, Baisselcaninae was an objective synonym of Elcaninae (Gorochov et al., 2006). These authors renamed Elcaninae sensu Gorochov as the new subfamily Archelcaninae. This means that Elcaninae only contains species from the Late Jurassic to Cretaceous and Archelcaninae contains all Early Jurassic elcanids (and some Middle Jurassic to Early Cretaceous species). This also means that the generic name *Panorpidium* (which is now in the subfamily Elcaninae) is not valid for Early Jurassic species which are morphologically dissimilar to the younger species. The authors also suggested that revision of Early Jurassic species previously attributed to *Panorpidium* ('*Elcana*') was necessary.

The family Locustopseidae was erected by Handlirsch (1906) for *Locustopsis elegans* Handlirsch, 1906, *L. dobbertinensis* Handlirsch, 1906 and *L. elongata* Handlirsch, 1906 from the Lower Toarcian of Dobbertin, Germany. *Gomphocerites bernstorffi* Geinitz, 1880 was transferred to *Locustopsis* as was *Gryllus bucklandi* Brodie, 1845 but the latter only tentatively. *L. lacoei* Cockerell, 1915 was described from the Lacoe Collection of British Lias insects held in the US, another of these specimens was identified as *L. bucklandi*, and *L. elegans* was designated as the genotype (Cockerell, 1915). Further species from England were described as *L. cockerelli* Handlirsch, 1939 (previously the specimen of *L. bucklandi* from Cockerell, 1915), *L. spectablis* Zeuner, 1942, *L. uvarovi* Zeuner, 1942, *L. gracilis* Zeuner, 1942, *L. constricta* Zeuner, 1942 and *Brodiana cubitalis* Zeuner, 1942 from the upper Rhaetian Lilstock Formation, Lower Hettangian Blue Lias Formation and Upper Sinemurian Charmouth Mudstone Formation. *Brodiana* was then synonymised with *Locustopsis* by Sharov (1968).

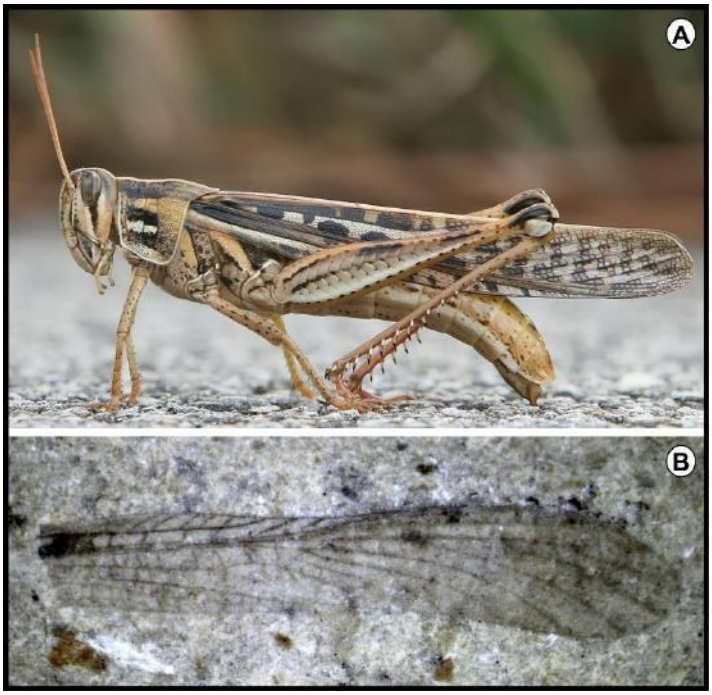

Figure 3.20. Examples of grasshoppers of the suborder Orthoptera: Caelifera. A. Extant grasshopper, *Schistocerca americana* (photo by Tom Friedel). B. Triassic grasshopper, *Locustopsis lacoei* (NHMUK I.11738).

The family has been previously revised (Zessin, 1983a) and *L. nana* and ? *L. dubia* were considered *nomen dubia* based on the fragmentary state of the holotypes. Several new genera were erected, and new species were described in *Locustopsis* from the Posidonia Shale Formation of Germany: *L. pulchella* Zessin, 1983a, *L. lacera* Zessin, 1983a, *L. gyra* Zessin, 1983a, *L. procera* Zessin, 1983a, *L. sippeli* Zessin, 1983a, and *L. mecklenburgica* Zessin, 1983a. *L. kruegeri* Zessin, 1983b was described in a separate paper (Zessin, 1983b).

The Jackson collection from the Sinemurian Charmouth Mudstone Formation of Dorset in England was examined by Whalley (1985), new specimens of *L. spectablis* were identified and *Orichalcum ornatum* Whalley, 1985 was described in the family Triassomantidae. Several of the specimens Zessin had worked on in 1983 were later readdressed (Zessin, 1988), *Plesioschwinzia* Zessin, 1988 was erected for *P. thalassophila* Zessin, 1988 and *L. reticulata* was transferred to this genus. Based on material from Germany Ansorge (1996) synonymised *L. magnifica, L. dobbertinensis* and *L. bernstorffi* making the latter the senior synonym and he added more material to *L. gyra*. Locustopsoidea was transferred to Acrididea (Gorochov, 2005). Cretaceous Orthoptera have been reviewed (Gorochov et al., 2006), and new species of locustopseids were described alongside descriptions of some older species. It was suggested that *L. dobbertinensis* and *L. magnifica* may actually belong to *Mesolocustopsis* based on cubital vein arrangement and they transferred *Orichalcum* to Locustopseinae commenting that it may actually be an aberrant *Locustopsis*.

Systematic Palaeontology

Order ORTHOPTERA Olivier, 1789

Suborder ENSIFERA Chopard, 1921

Superfamily OEDISCHIOIDEA Handlirsch, 1906

Family BINTONIELLIDAE Handlirsch, 1939

Subfamily BINTONIELLINAE Handlirsch, 1906

Genus HAGLOPSIS Handlirsch, 1906

1906 *Haglopsis* Handlirsch, 426.

1939 *Bintoniella* Handlirsch, 55

1915 *Haglopsis* Handlirsch; Cockerell, 474.

1968 *Bintoniella* Handlirsch; Sharov, 41 (39 in 1971 English translation)

1982 *Bintoniella* Handlirsch; Whalley, 143.

1992 *Bintoniella* Handlirsch; Carpenter, 162.

Type species.—*Haglopsis parallela* (Giebel, 1856).

Emended d*iagnosis.*—Rs with four to six posteriorly pectinate branches.

Description.—In forewing, Sc terminates on the costal margin in apical third of wing length; R terminates just before the apex; R diverges from Rs at or near the middle of the wing; Rs with four to six posteriorly pectinate branches. M branches anteriorly from CuA+CuP1 anterior branch at one quarter the length of the wing and immediately divides into simple MA and MP (straight) which terminate on the posterior margin before the wing apex. CuA+CuP1 anterior branch bifurcates at least once. and the two branches are simple or may bifurcate again. CuP1 posterior branch simple. CuP2 simple and straight, forming a claval furrow. Three A veins, 1A and 2A are simple, 3A simple or branched. Many closely spaced crossveins.

Remarks.—*Haglopsis* Handlirsch, 1906 and *Bintoniella* Handlirsch, 1939 are clearly the same genus even though the former was transferred to the family Haglidae by Handlirsch (1906) and the latter was used to erect the family Bintoniellidae by Handlirsch (1939). The monospecific *Bintoniella* Handlirsch, 1939 is therefore a junior synonym of *Haglopsis* Handlirsch, 1906 by priority and *Haglopsis* becomes the type genus of the family. The family name Bintoniellidae is still valid according to the ICZN Code (Article 40) even though the name of the type genus has now changed. Bintoniellidae are clearly distinct from Haglidae, the latter having the more derived ensiferan character of stridulatory apparatus on the male wings; *Hagla* Giebel, 1856 is the type genus of the latter family.

Haglopsis parallela (Giebel, 1856)

1845 '*Chauliodes*' Brodie, 102, pl. 8, fig. 5, pl. 10, figs 6, 9.

1856 *Orthophlebia parallela* Giebel, 260.

1856 *Orthophlebia longissima* Giebel, 260 1879 *Orthophlebia longissima* Giebel; Goss, 145.

1879 *Orthophlebia parallela* Giebel; Goss, 145.

1891 *Orthophlebia longissima* Giebel; Scudder, 157, No. 1030.

1891 *Orthophlebia parallela* Giebel; Scudder, 157, No. 1033.

1893 *Orthophlebia longissima* Giebel; Woodward, 367.

1893 *Orthophlebia parallela* Giebel; Woodward, 367.

1906 *Haglopsis parallela* (Giebel); Handlirsch, 426, pl. 40, fig. 13.

1906 *Orthophlebia longissima* Giebel; Handlirsch, 504.

1915 *Haglopsis parallela* (Giebel); Cockerell, 474, pl. 60, fig. 3.

1939 *Bintoniella brodiei* Handlirsch, 55, pl. 4, fig. 65

1939 *Orthophlebia longissima* Giebel; Handlirsch, 150, fig. 306.

1968 *Bintoniella brodiei* Handlirsch; Sharov, 42 (41 in 1971 English translation), fig. 16C.

1982 *Bintoniella brodiei* Handlirsch; Whalley, 145–7, figs 1–3, 5–6.

1992 *Bintoniella brodiei* Handlirsch; Carpenter, 162.

2012 †*brodiei* Handlirsch; Béthoux, 199, 204, 207, 218, figs 24 A, B, N–P, 25 A–E.

Holotype.—NHMUK II.3098 (Fig. 3.21). Brodie coll. from either Hasfield, Strensham or Bidford (Rhaetian or Hettangian).

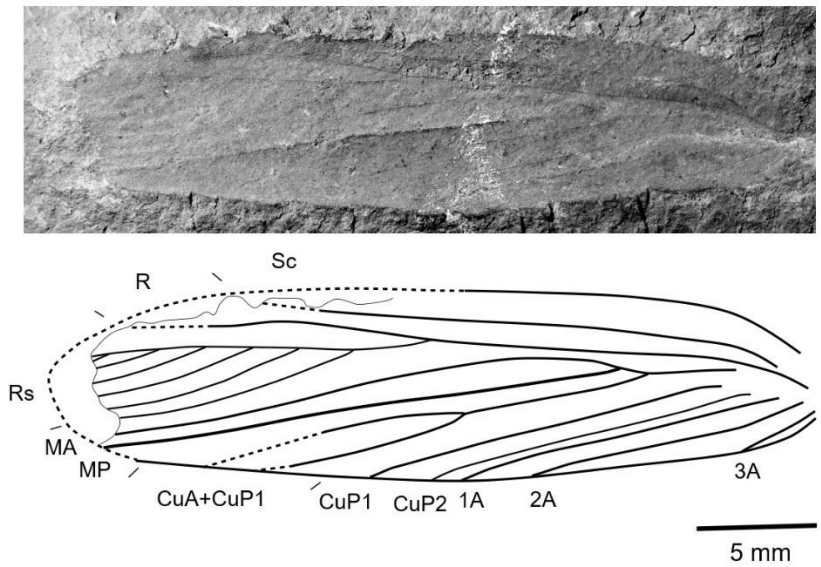

Figure 3.21. Holotype of *Haglopsis parallela* (Giebel, 1856) (NHMUK II.3098), modified from Kelly and Ross (In preparation d).

Remarks.—The holotype of *Haglopsis parallela* (Giebel, 1856) was not labelled in the NHM collection but an unnumbered forewing specimen matches the figure in Brodie (1845, pl. 10 fig. 9), particularly in being the only specimen with pigmented veins that has six branches of Rs, and a missing tip making it appear more rounded as indicated in the original figure. There is faint writing in ink on the rock which is consistent with Brodie's practice of writing notes directly on his specimens. With the aid of a UV pen this appears to read '*Orthophlebia*' which was the earlier generic identification of the specimen. It has been given a new number, though it may have been registered in the past and the original number and label were subsequently lost. The locality of this specimen was not specifically recorded but the specimens of '*Chauliodes*' mentioned in Brodie (1845) came from Hasfield, Strensham and Bidford and so the holotype is likely to be either Rhaetian or Hettangian.

Additional material.—Rhaetian: NHMUK I.10437/I.10446 (pt and cpt), I.11109, I.11237 Strensham; I.10644 Wainlode. 32692 is only recorded as 'Worcestershire' and so the exact age is unknown.

Isolated forewings: Rhaetian: NHMUK I.3310, I.10592 Brown's Wood; I.10641 Forthampton; I.10439, I.10443, I.10447, I.10457, I.10532, I.10538 (pt and cpt), I.10539, I.10542, I.10554 (Whalley, 1982, fig. 5), I.10692, I.11112 Strensham. Hettangian: NHMUK I.6652, I.6654, I.6656 (pt and cpt) (Whalley, 1982, fig. 6; Béthoux, 2012, figs 24N–P), I.6659 (pt and cpt), I.6661, I.6772, I.6773, I.6781, I.6783, I.6785, I.10463 (Brodie, 1845 pl. 10, fig. 6; holotype of *Bintoniella brodiei* Handlirsch, 1939; Whalley, 1982, fig. 3; Béthoux, 2012, figs 24A–B), I.10578, I.11080, OUMNH J.23721, WARMS G.390 Binton; NHMUK I.10668/I.10669 (Béthoux, 2012, figs 25A–B) [Béthoux, 2012 considered this was a hindwing however it has a branching CuA+CuP1 anterior branch] Stratford on Avon. Sinemurian: BGS C.S.E. 6178/6179 (pt and cpt) (Whalley, 1982, figs 1, 2) Western English Channel. Unknown: NHMUK I.11729, I.15002; USNM 61393 (Lacoe: 3489 (Cockerell, 1915, pl. 60, fig. 3) 3430, 3431) from unknown localities in England.

Isolated hindwings: Rhaetian: NHMUK I.10588, I.10616 Brown's Wood; I.10543, I.10534/I.10558 (pt and cpt), I.10536 (pt and cpt) (Béthoux, 2012, figs 25C–E), OUMNH J.55135 Strensham; II.2068 Wainlode Cliff. Hettangian: I.6766/I.6683 (pt and cpt), I.10583 Binton; I.3538 Bickmarsh (holotype of *Orthophlebia longissima* Giebel, 1856, Handlirsch, 1939, fig. 306). Rhaetian-Hettangian: I.10666 Highnam.

Emended d*iagnosis.*—Forewing (tegmen) length 21–44 mm, width 5–13 mm, with pigmented veins and colour spots or bands; CuA+CuP1 anterior branch bifurcated; may be a further bifurcation on either anterior or posterior branch.

Description.—Forewing as for generic description and species diagnosis. Hindwing similar to forewing with pigmented veins and pterostigma, but with a more pointed apex and a simple CuA+ CuP1 anterior branch. NHMUK I.11237 also preserves some of the body and head; forefemur straight; foretibia slightly expanded apically; three or four tarsal segments preserved, at least basal two are bilobed, most basal section is longer than the others; mesotarsi three segmented similar to forelegs with possible tarsal claws. Head with large eye preserved; elongate mandibles with right jaw larger than left, right jaw appears toothed but no indication of this on left jaw, curved outer edge, sharply pointed apically.

Remarks.—Many of the figures from Brodie (1845) were later named by Giebel (1856) without further examination of the specimens. Thus, *Orthophlebia longissima* Giebel, 1856 and *Orthophlebia parallela* Giebel, 1856 were named based on Brodie's pl. 8, fig. 5 and pl. 10, fig. 9 respectively. The holotype of *O. longissima* is a poorly preserved hindwing though it is conspecific with *O. parallela*, which is a nearly complete forewing, so the latter is here chosen as the senior synonym. *O. parallela* was recognised as belonging to Orthoptera and placed in the new genus *Haglopsis* Handlirsch, 1906. An additional specimen of this species was figured by Cockerell (1915).

Bintoniella brodiei Handlirsch, 1939 was named based on another figure in Brodie (1845, pl. 10, fig. 6). From studying all available specimens and re-discovering the holotype of *H. parallela* it is clear that *Haglopsis parallela* (Giebel, 1856) and *Bintoniella brodiei* Handlirsch, 1906 are conspecific with the first name having date priority. There could be a case for suppression of *H. parallela* given that this species name has barely been used since however there is a problem in that another species was named as *Haglopsis brodiei* Cockerell, 1915 (thus homonymous with *B. brodiei* Handlirsch) which we agree is a separate species (see below), so we prefer to retain *Haglopsis parallela* (Giebel, 1856) as the correct name for this species.

Haglopsis brodiei Cockerell, 1915

1915 *Haglopsis brodiei* Cockerell, 474, pl. 60, fig. 7.
1939 *Haglopsis ?brodiei* Cockerell; Handlirsch, 57.

Holotype.—USNM 61392 (Lacoe 3453) (Fig. 3.22), Lacoe coll., Planorbis Zone, Blue Lias Formation; Lower Lias: Lower Hettangian; Binton, Warwickshire.

Additional material.—

Forewings: Rhaetian: NHMUK I.10484 Wainlode Cliff. Hettangian: I.3356, I.3375, I.3383 (Béthoux, 2012, figs 24H–I), I.3384 (pt and cpt), I.6660, I.6770, I.6784 (Whalley, 1982, fig. 4; Béthoux, 2012, figs 24C–E), I.10464 (Béthoux, 2012, figs 24F–G), WARMS: G.305, G.8145 Binton;

I.10495, I.11217 Temple Grafton. Unknown: NHMUK I.6790 (Béthoux, 2012, figs 24K–M) is from ‘Climber’.

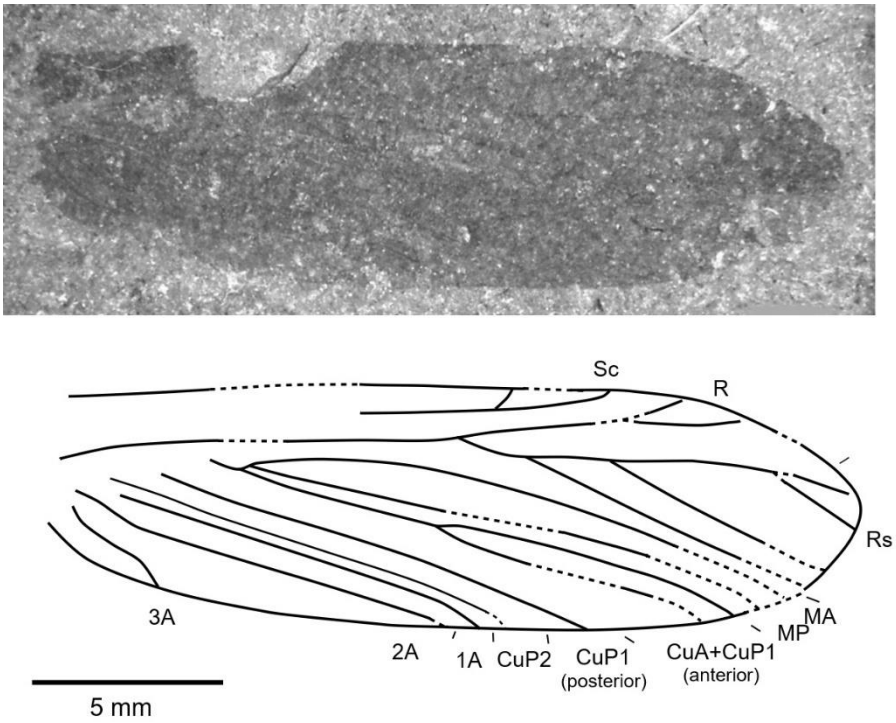

Figure 3.22. Holotype of *Haglopsis brodiei* Cockerell, 1915 (USNM 61392, Lacoe 3453), modified from Kelly and Ross (In preparation d).

Hindwings: Hettangian: NHMUK I.474, I.6701 (pt and cpt), I.6768, I.6779, (Béthoux, 2012, figs 25F–G), I.6780, I.10479, I.10585, I.10587, I.10933, I.10935 Binton; I.6799 Temple Grafton. Unknown: NHMUK I.15012 (pt and cpt) from an unknown locality in England.

Emended diagnosis.—Forewing (tegmen) length 15.5–33 mm, width 4.5–9 mm; strongly and evenly pigmented; CuA+CuP1 posterior branch bifurcated once.

Description.—Forewing as for generic description and species diagnosis. *H. parallela* shows some variation in the number of bifurcations of CuA+CuP1 anterior branch, but this is not seen in any specimen of *H. brodiei*. Hindwing similar to forewing in that it is strongly and evenly pigmented, but with a more pointed apex and a simple CuA+CuP1 anterior branch.

Remarks.—There are clearly two forms of *Haglopsis* in the collection at the NHM, the typical form of *H. parallela* (=*Bintoniella brodiei* Handlirsch) has pigmented veins and spots, and the other form is strongly pigmented with the pigment evenly distributed across the entire fore– and hindwings. A specimen of the pigmented form was named as *Haglopsis brodiei* Cockerell, 1915. The two forms have been considered as sexual dimorphs (Whalley, 1982), males having the pigmented veins and

spots and females being evenly and more strongly pigmented. Although Carpenter (1992) suggested that males were the more heavily sclerotized forms, Béthoux (2012) accepted the opinion of Whalley (1982). When the localities are considered, however, there is a marked difference.

Most of the Rhaetian specimens are from Strensham (18 specimens) and most of the Hettangian specimens are from Binton (37 specimens). Although the specimens from Binton show both forms in roughly equal amounts (17 with pigmented veins and spots, 20 evenly pigmented), the specimens from Strensham only have pigmented veins and colour spots, so it seems very unlikely that only one sex would be preserved at the latter locality. The variation is not an artefact of splitting the rocks as those specimens with both part and counterpart show the same pigmentation on both. There is only one evenly pigmented specimen of Rhaetian age, from Wainlode Cliff (NHMUK I.10484), so this form was extremely rare prior to the TJB. When size is considered, if *H. parallela* (Giebel, 1856) and *H. brodiei* Cockerell, 1915 were the same species then there is a huge size range with the largest being three times the size of the smallest (Fig. 3.23), which seems unlikely. The evenly pigmented forms are generally smaller than the ones with pigmented veins and spots, but they have overlapping size ranges. These differences in size and stratigraphy lead us to regard *H. parallela* (Giebel, 1856) and *H. brodiei* Cockerell, 1915 as separate species.

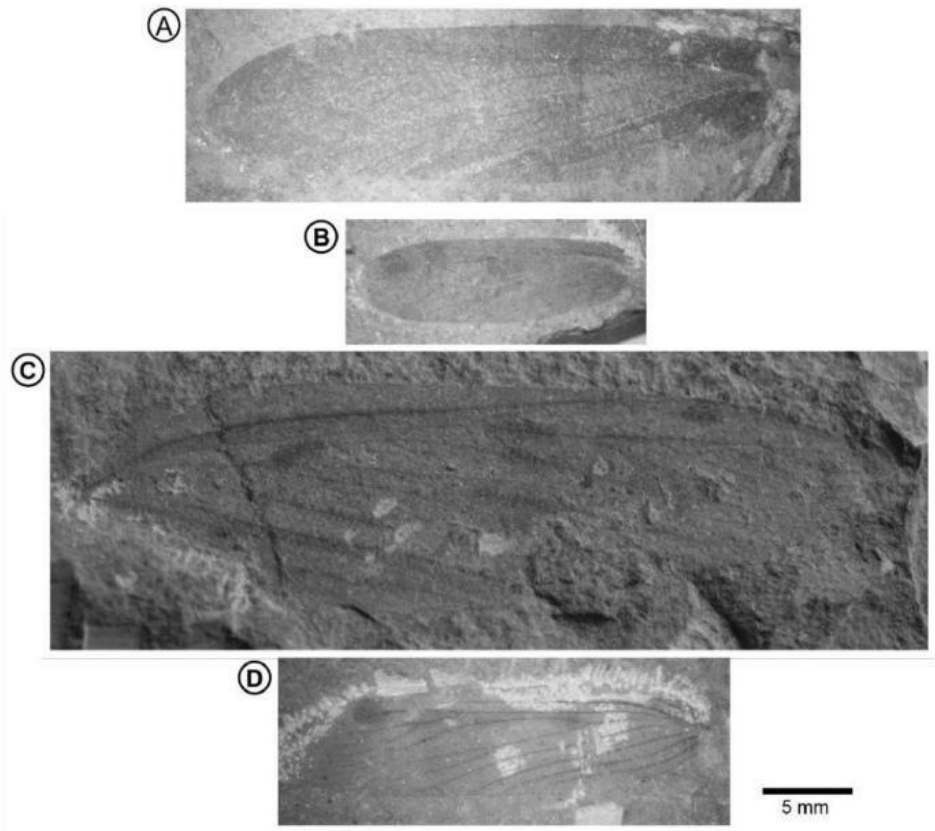

Figure 3.23. Size comparison of *H. parallela* and *H. brodiei*. A) Largest *H. brodiei* I.10464; B) Smallest *H. brodiei* I.3384; C) Largest *H. parallela* I.6783 and D) Smallest *H. parallela* I.6781. All specimens are prefixed NHMUK. For Kelly and Ross (In preparation d).

Superfamily HAGLOIDEA

Family HAGLIDAE

Genus “Orth:Hag. gen. nov.”

Type species.—“Orth:Hag. gen. et sp. nov.”

Diagnosis.—Third branch of MA basal to main fork; four branches of Rs; relatively simple Cu forking; R bifurcates twice.

Remarks.—This genus seems to lie morphologically between *Hagla* and *Prohagla* Riek, 1954 (venation diagram, Gorochov (1995), figs 290, 291) which is only known from the Late Triassic of Australia (Riek, 1954, 1955). There are 4 Rs branches in the new genus and *Prohagla* but 5–6 in *Hagla*; in *Prohagla* Rs curves towards the apex whereas it is straight in the new genus which is more like *Hagla*. Also, in *Prohagla* R is anteriorly pectinate whereas in the new genus R bifurcates and then the posterior branch bifurcates again and in *Hagla* R bifurcates and then the posterior branch bifurcates twice. In *superba* the costal area narrows sharply at around the midwing whereas in the new genus and *Hagla* the decrease in width is much more gradual. CuP curves towards anterior margin in *Hagla* and ‘new genus’ but towards posterior margin in superba. The free 3rd branch of MA is unique. The 3rd anterior cubital branch in ‘new genus’ is much more distal to the crossvein than in *P. superba* and the middle branch is not forked (in *Hagla* this middle branch is forked twice).

“Orth:Hag. gen. et sp. nov.”

Holotype.—NHMUK I.6696 (Fig. 3.24), ‘Insect limestone’ of the Planorbis Zone (Lias Group: Blue Lias Formation: Wilmcote Limestone Member); Early Jurassic: Lower Hettangian; Binton, Warwickshire.

Paratype.—NHMUK I.10531, ‘Insect limestone’ of the *Pseudomonotis* beds (Penarth Group: Lilstock Formation); Late Triassic: upper Rhaetian; Strensham, Worcestershire.

Diagnosis.—As for genus, monospecific.

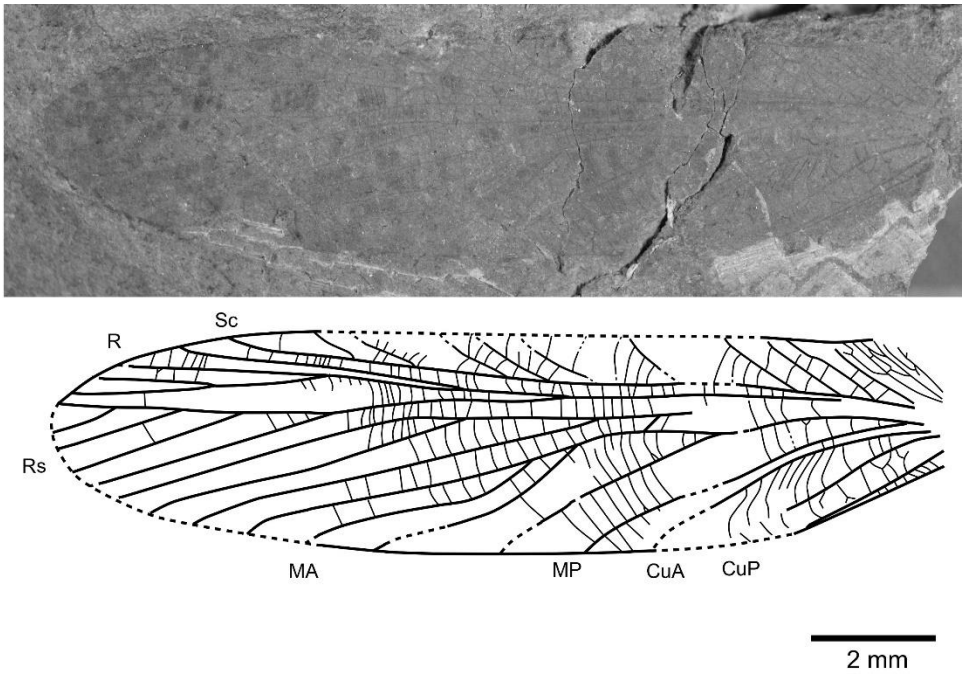

Figure 3.24. Holotype of "Orth:Hag. gen. et sp. nov." (NHMUK I.6696), figure prepared for Kelly and Ross (In preparation d).

Superfamily ELCANOIDEA Handlirsch, 1906

Family ELCANIDAE Handlirsch, 1906

Subfamily ARCHELCANINAE Gorochov et al., 2006

Type genus.—Archelcana Sharov, 1968

Remarks.—Gorochov et al. (2006) indicated that Early Jurassic elcanids should all be in the subfamily Archelcaninae and that the Elcaninae (including *Panorpidium*) are only upper Jurassic or Cretaceous and are characterised by a fusion of the distal parts of CuA2, CuP and 1A.

Genus ARCHELCANA Sharov, 1968

Type species.—Elcana britannica Handlirsch, 1939

Emended diagnosis.—May have branches of C depending on preservation; base of MA1 is continuous with base of RS which appears as a cross-vein between R and the main Rs+M+Cu branch; Rs is variable and characteristic of the different species.

Remarks.—*Archelcana* was described based on the absence of branches of C, the slanted nature of C, the position of MA1 distal to the base of Rs and the presence of two anal veins compared with *Panorpidium* (‘*Elcana*’) (Sharov, 1968 followed by Carpenter, 1992). *Archelcana* with *Elcana* were synonymised (Zessin, 1987) based on C branches being too weakly defined due to preservation and that the course of C, variation of anal branches and the placement of MA in relation to Rs are all seen in other species of *Elcana*. Additionally, Sharov did not notice that the holotype of ‘*Panorpidium liasina*’ does not have C branches, probably because it has not been figured since Brodie (1845) even though Giebel, Handlirsch, Cockerell, and Zessin have all revised or discussed the species. Whalley (1985) described *A. durnovaria* but indicated that the presence (not the absence) of C branches was diagnostic for the genus. Zessin has previously indicated C branches may or may not be present depending on preservation and the anal and radial sectors are variable at genus level.

Archelcana liasina (Giebel, 1856)

1845 ‘Ephemera’ Brodie, pp. 102, 127, pl. 10, fig. 14. 1856 *Rapha liasina*, Giebel, p. 290.
1886 *Rapha liasina*, Giebel; Deichmüller, p. 17.
1906 *Elcana liasina* (Giebel); Handlirsch, p. 414.
1906 *Elcana britannica*, Handlirsch, p. 414, pl. 39, fig. 28.
1906 *Elcana Brodiei*, Handlirsch, p. 414.
1985 *Archelcana durnovaria*, Whalley, p. 127, figs 11–15.
1915 *Elcana brodiei* (Handlirsch); Cockerell, pp. 472–473.
1939 *Elcana angustior*, Handlirsch, p. 37, pl. 2, fig. 26.
1968 *Archelcana britannica,* Sharov, p. 118, fig. 14F.
1987 *Elcana liasina* (Giebel); Zessin, p. 31,
2006 *Archelana liasina* (Giebel); Gorochov et al. p. 642, fig. 1A.

Holotype.—NHMUK I.11676 (Fig. 3.25), Bed 18, (Lilstock Formation: Cotham Member); Late Triassic: upper Rhaetian; Strensham, Worcestershire.

Additional material.—Rhaetian: NHMUK: I.11045, I.11066, I.11068 Brown’s Wood; I.10821, I.10489 Charfield; I.11115, I.10706, I.10452 Strensham; In.49294 Wainlode Cliff; I.11257, I.11005 Westbury. Hettangian: NHMUK I.6792, I.10579, I.6702, I.11251, I.10470, I.10476, I.3376, I.3366, I.6684, I.10473, I.3362, I.6658, I.6667, I.6686, I.6672, I.11249, I.6673, I.6687, I.6655, I.6680, I.6688 Binton; I.10636 Bidford; I.10493 Wilmcote; WARMS: G 8157 Wilmcote; G 408 Stratford–upon– Avon; G 8146 1, G 8146 2, G 8146 3. Sinemurian: NHMUK PI II 2192 a,b, PI II 2195, PI II 2194, PI II 2191 a,b, PI II 2193 a,b, In. 64005, In. 53976, In.64038, In.59162 Black Ven; In.53922, In.59381, In.59377,

In.59139 Stonebarrow. Unknown: NHMUK I.3560, I.11676, I.33764, I.10708; USNM 61389 (Lacoe numbers: 3490, 3491, 3493, 3494, 3495) all from unknown locality in England.

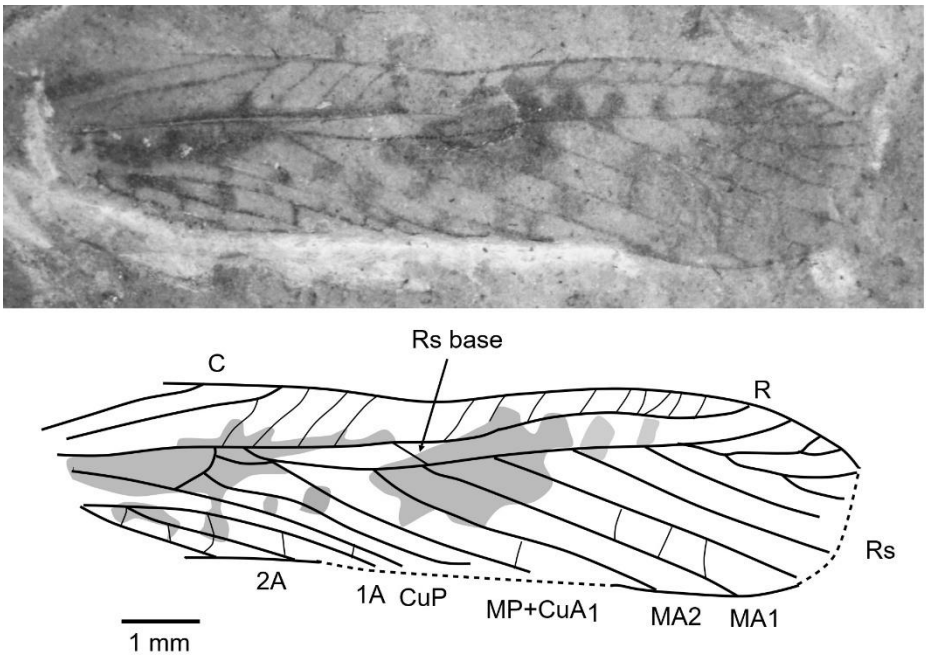

Figure 3.25. Holotype of *Archelcana liasina* (Giebel, 1856) (NHMUK I.11676), for Kelly and Ross (In preparation d).

Emended diagnosis.—Radial sector is variable and may have seven or eight branches reaching the margin. Anal region is also variable with either three or four veins present although this may be due to preservation as the fourth anal vein can be faint. MP and CuA1 are fused along their length. C branches may or may not be present depending on preservation.

Description.—Holotype, forewing length 11 mm, width 2.5 mm. MA1 is slightly posterior to the base of Rs but this is not seen in all specimens and is thought to be a form of intraspecific variation in both similar genera. Sword shaped ovipositor preserved in I.6702. Anal region is variable in those specimens with it preserved but, in many specimens, the anal region has broken off, so assignment is based on similarities in the remainder of the wing.

"Orth:Elc. sp. nov."

Holotype.—NHMUK I.11246 (Fig. 3.26) Brodie Coll., Bed 18; (Lilstock Formation: Cotham Member); Late Triassic: upper Rhaetian; Strensham, Worcestershire.

Additional material.—NHMUK I.11704 from unknown locality in England (only apical section preserved).

Diagnosis.—Forewing characters, length c. 13 mm, width c. 4 mm. Five anal veins, MP and CuA1 are not fused and Rs has five main oblique branches leaving Rs, but up to 10 branches reaching the margin.

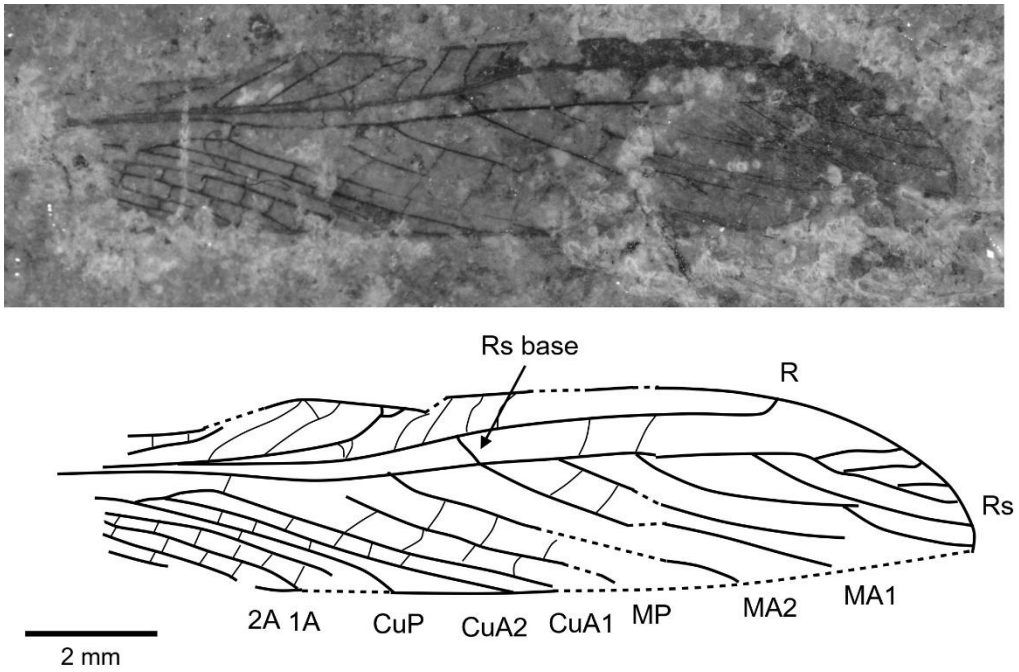

Figure 3.26. Holotype of "Orth:Elc. sp. nov." (NHMUK I.11246), figure prepared for Kelly and Ross (In preparation c).

Description.—Preserved length 13 mm, preserved width 3 mm.

Remarks.—There is intraspecific variation present in the radial and anal regions of *A. liasina* but there are no examples of specimens with the 'extra vein' in the M region which is thought to represent the unfused MP and CuA1 veins.

Archelcana geinitzi (Heer, 1880)

Holotype.—MBI 15.1a,b (Museum für Naturkunde, Berlin), Griefswald Coll., offshore claystone; Early Jurassic: Toarcian; Dobbertin, Mecklenburg.

Additional material.—New material from England: NHMUK: I.11295 (Fig. 3.27), I.11417 Alderton, Gloucestershire; I.11427, I.3349, I.11334 Dumbleton, Gloucestershire (all Toarcian).

Diagnosis.—Four anal veins; 1A, CuP, and CuA2 much closer together than in other species in the genus. Kink in C.

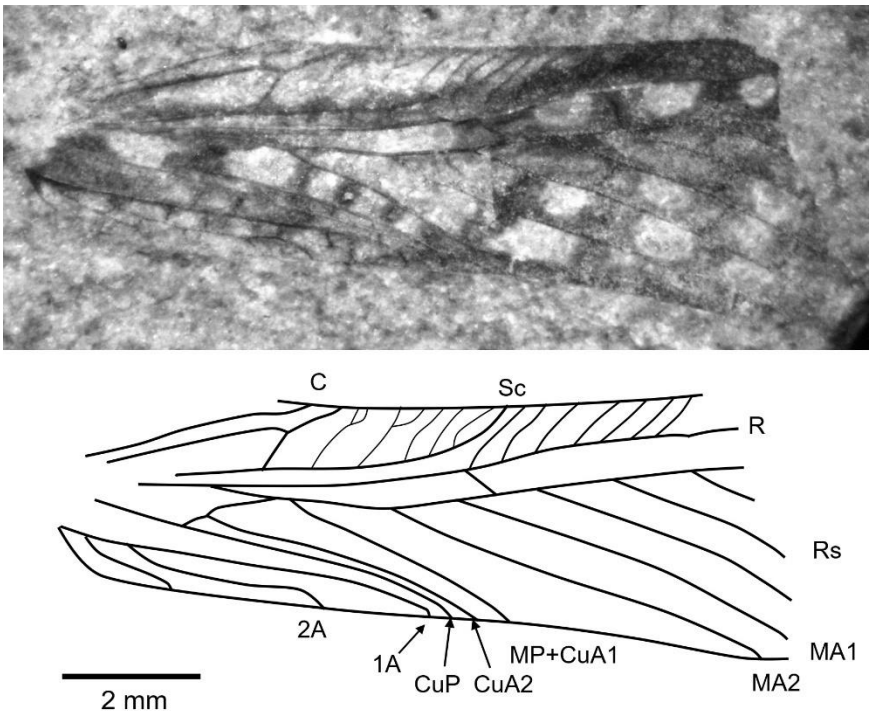

Figure 3.27. An English specimen of *Archelcana geinitzi* (Heer, 1880) (NHMUK: I.11295), for Kelly and Ross (In preparation c).

Remarks.—The holotype of this species has not been examined in person, only new specimens were added from the Toarcian of England extending the geographic range of this species. The specimens are fragmentary and so it is difficult to provide a size range for the English specimens.

Suborder CAELIFERA ander, 1939

Superfamily LOCUSTOPSOIDEA Handlirsch, 1907

Family LOCUSTOPSEIDAE Handlirsch, 1907

Diagnosis.—From Gorochov et al. (2006). Forewing characters: CuA2 base displaced from basal part of tegmen; MP+CuA1 with one to three branches.

Subfamily LOCUSTOPSEINAE Handlirsch, 1907

Type genus.—Locustopsis Handlirsch, 1907.

Diagnosis.—From Gorochov et al. (2006). Long Sc; two or three distinct branches of MA.

Genus LOCUSTOPSIS Handlirsch, 1907

Type species.—L. elegans Handlirsch, 1907.

Diagnosis.—From Gorochov et al. (2006). Three branches of MA (primitive position of the posterior branch of MA1); two branches of MP+CuA1.

Remarks.—The type specimen for this genus is damaged (EMAUG 122/2, Fig. 3.28) and it is difficult to ascertain whether MP+CuA1 has one or two branches. The original figure by Handlirsch (1906–08, pl. 40, fig. 1) shows the diagnostic two branches of MP+CuA1 but this figure is not entirely accurate, so it is impossible to know if this is actually the case. The species was refigured after Handlirsch by Zessin (1983a, fig. 16). It is possible that there are two branches, in which case the original diagnosis for *Locustopsis* is sound, but it may be that there is only one branch of MP+CuA1 which would mean that *Mesolocustopsis*, which is defined as having MA similar to *Locustopsis* but with a single branch of MP+CuA1, is not a valid genus and actually a junior synonym of *Locustopsis*. It is difficult to say with certainty given the evidence currently available. The species has not been collected from British deposits, so we cannot provide further details from the British material, but further examination of the German material may shed some light on the correct tegminal venation of this genus if further examples can be found. For the purposes of our revision of the English locustopseids we retain the original diagnosis for the genus.

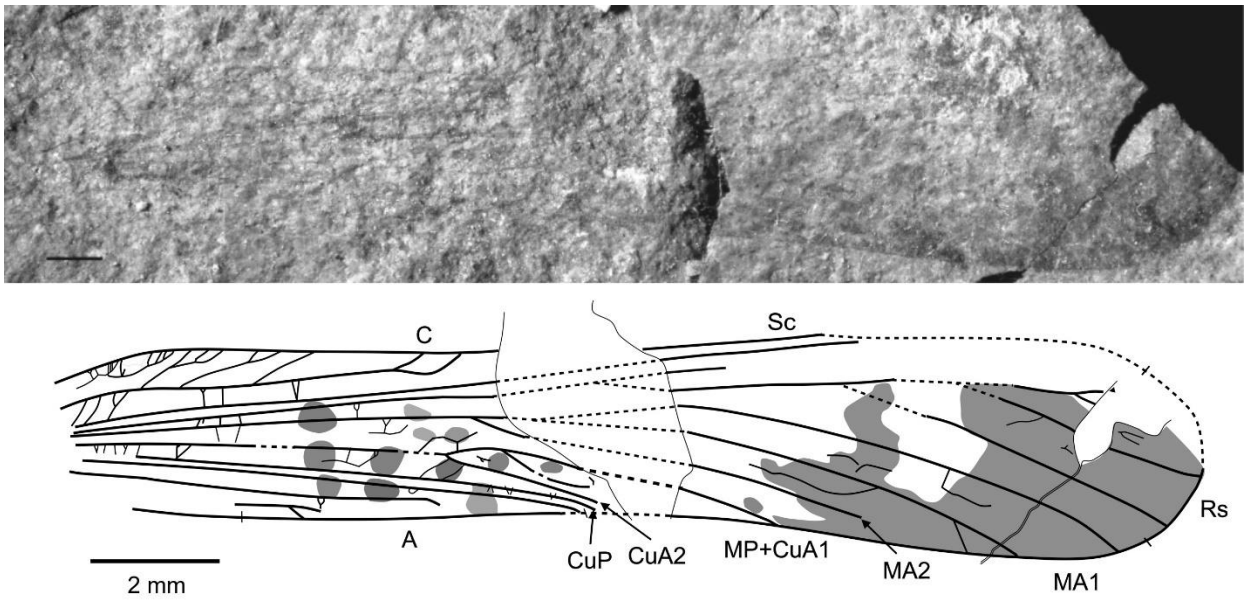

Figure 3.28. Holotype of *Locustopsis elegans* Handlirsch, 1907 (EMAUG 122/2), for Kelly and Ross (In preparation b).

Locustopsis lacoei (Cockerell, 1915)

1915 *Locustopsis lacoei* Cockerell, p. 473, pl. 60, fig. 4.

1939 *Locustopsis* "*Lacoi*" Cockerell; Handlirsch, p. 34.

1942 *Locustopsis lacoei* Cockerell; Zeuner, p. 12.

1942 *Locustopsis uvarovi* Zeuner, p. 10, fig. 2.

1983a *Locustopsis uvarovi* Zeuner; Zessin, p. 182, fig. 7.

1983a *Locustopsis lacoei* Cockerell; Zessin, p. 185, fig. 10.

1991 *Locustopsis lacoei* Cockerell; Zessin, table 1.

1991 *Locustopsis uvarovi* Zeuner: Zessin, table 1.

1998 *Locustopsis lacoei* Cockerell; Martins-Neto, p. 134, fig. 1.

1998 *Locustopsis uvarovi* Zeuner; Martins-Neto, p. 134, fig. 1.

Holotype.—USNM 61390 (Lacoe number 3460) (Fig. 3.29), 'Insect limestone' of the Planorbis Zone (Lias Group: Blue Lias Formation: Wilmcote Limestone Member), Lower Hettangian; Early Jurassic of Binton, Warwickshire.

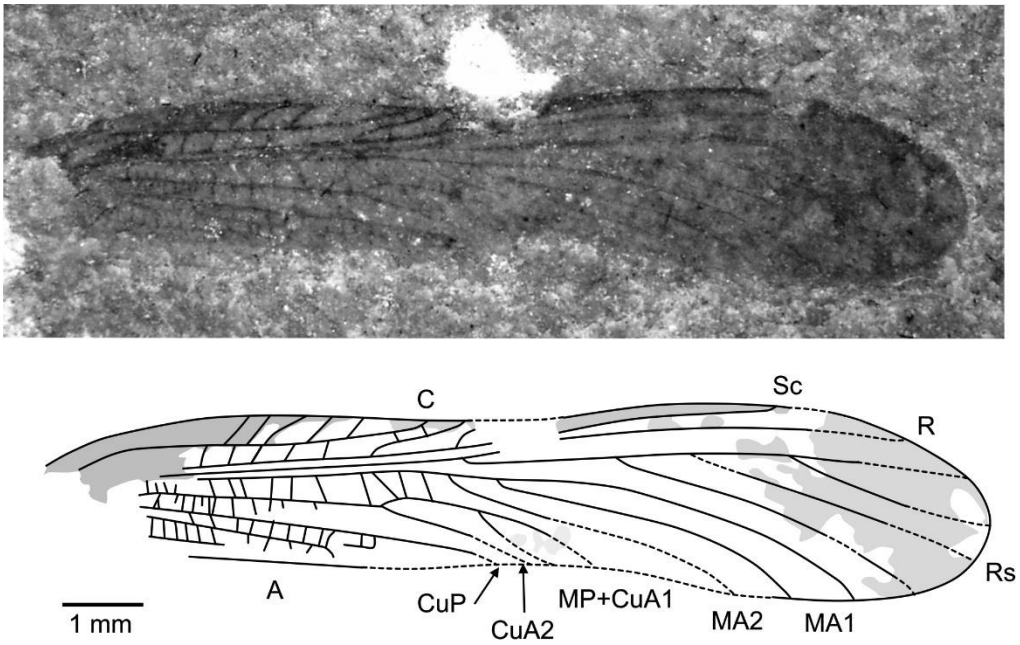

Figure 3.29. Holotype of *Locustopsis lacoei* (Cockerell, 1915) (USNM 61390, Lacoe number 3460), for Kelly and Ross (In preparation b).

Additional material.—NHMUK I.11738, I.10561 Strensham (Rhaetian); I.11814 and I.11699 (holotype of *L. uvarovi*, Fig. 3.30) from an unknown locality in England.

Emended diagnosis.—Forewing characters, length 12–16 mm, width 1.6–1.9 mm. Combination of branching Sc, four branches of Rs, MA1 bifurcates, MA2 simple, MP+CuA1 bifurcates, CuA2 simple; C meets anterior margin after MP+CuA1 splits from CuA2; membrane colouration.

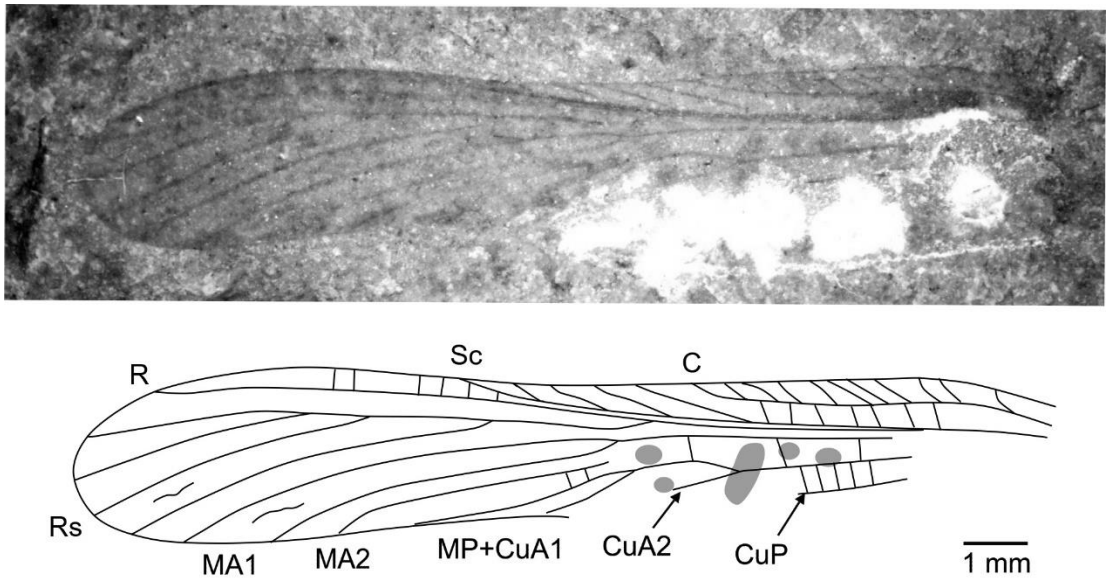

Figure 3.30. *Locustopsis lacoei*, holotype of *Locustopsis uvarovi* Zeuner, 1942 (NHMUK I.11699), for Kelly and Ross (In preparation b).

Description.—Holotype is a forewing, length c. 12 mm, width c. 1.8 mm and relatively well preserved. C pigmented with five anterior oblique branches, terminates just beyond basal third of wing. Sc with at least three branches. Rs originates in middle of wing. MA1 bifurcates in middle of wing; MP+CuA1 probably terminates just beyond two thirds the length of the wing. Pigmented at base and patchy pigmentation in distal half of wing.

Remarks.—L. lacoei was originally erected by Cockerell (1915) from the Lacoe collection held at the USNM based on a single branch of MP+CuA1. Although very faint and difficult to see, MP+CuA1 does appear to have two branches when different angles of light are applied under the microscope. *L. uvarovi* was described by Zeuner (1942) but it is very similar to *L. lacoei*. MP+CuA1 appears to be more curved in the holotype of *L. uvarovi* but it is not entirely preserved in *L. lacoei*. The holotype of *L. lacoei* is c. 12 mm in length whereas the holotype of *L. uvarovi* is c. 17 mm in length, but there are several specimens identified as *L. uvarovi* with a size range of c. 11 mm to 17 mm. The only discernible difference is that the colouration of *L. uvarovi* is spottier whereas that of *L. lacoei* is more blocked colour, but this could easily be due to intraspecific variation.

Locustopsis cubitalis (Zeuner, 1942)

1942 *Brodiana cubitalis* Zeuner, p. 14, fig. 8.

1968 *Locustopsis cubitalis* (Zeuner); Sharov, p. 92.

1983 *Locustopsis cubitalis* (Zeuner); Zessin, p. 185, fig. 11.

1991 *Locustopsis cubitalis* (Zeuner); Zessin, table 1.

1991 *Brodiana cubitalis* Zeuner; Carpenter, p. 177.

1998 *Locustopsis cubitalis* (Zeuner); Martins-Neto, p. 134, fig. 1.

Holotype.—NHMUK I.10672 (Fig. 3.31) 'Insect limestone' of the *Pseudomonotis* beds (Lilstock Formation: Cotham Member); Late Triassic: upper Rhaetian; Strensham, Worcestershire.

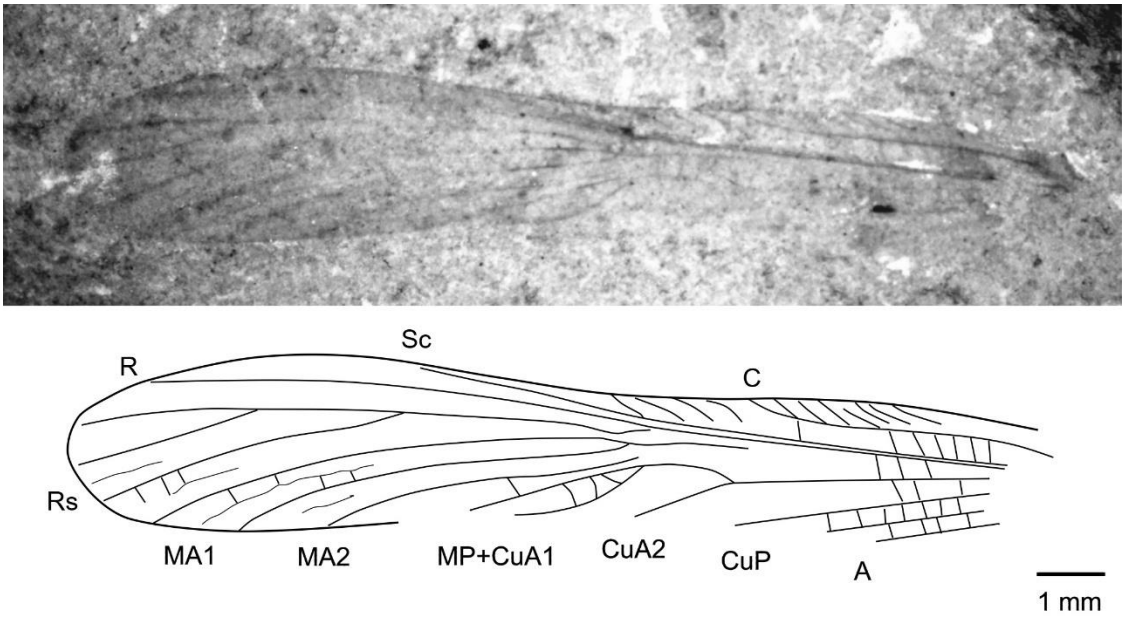

Figure 3.31. Holotype of *Locustopsis cubitalis* (Zeuner, 1942) (NHMUK I.10672), for Kelly and Ross (In preparation b).

Emended diagnosis.—Forewing characters known, length c. 16 mm, width c. 1.8 mm. Similar to other *Locustopsis* species except three branches of Rs; shorter C, meeting anterior margin before MP+CuA1 splits from CuA2; no membrane colouration but possible vein colouration.

Locustopsis spectablis (Zeuner, 1942)

1942 *Locustopsis spectablis* Zeuner, p. 8, fig. 1.

1983 *Locustopsis spectablis* Zeuner; Zessin, p. 182, fig. 6.

1985 *Locustopsis spectablis* Zeuner; Whalley, p. 137, fig. 26–28.

1991 *Locustopsis spectablis* Zeuner; Zessin, table 1.

1998 *Locustopsis spectablis* Zeuner; Martins-Neto, p. 134, fig. 1.

1999 *Locustopsis spectablis* Zeuner; Jarzembowski, p. 152, fig. 13C, D.

2010 *Locustopsis spectablis* Zeuner; Jarzembowski and Palmer, p. 174, fig. 4.27.

2010 *Locustopsis spectablis* Zeuner; Ross, p. 280.

Holotype.—NHMUK I.10563 (Fig. 3.32), 'Insect limestone' of the *Pseudomonotis* beds (Lilstock Formation: Cotham Member); Late Triassic: upper Rhaetian; Strensham, Worcestershire.

Paratype.—NHMUK I.10654 Copt Heath (Hettangian).

Emended diagnosis.—Forewing characters, length c. 25 mm Combination of branched Sc, six branches of Rs, MA1 bifurcated, MA2 simple, MP+CuA1 bifurcated, CuA2 simple. Pigmented veins but no further patterning.

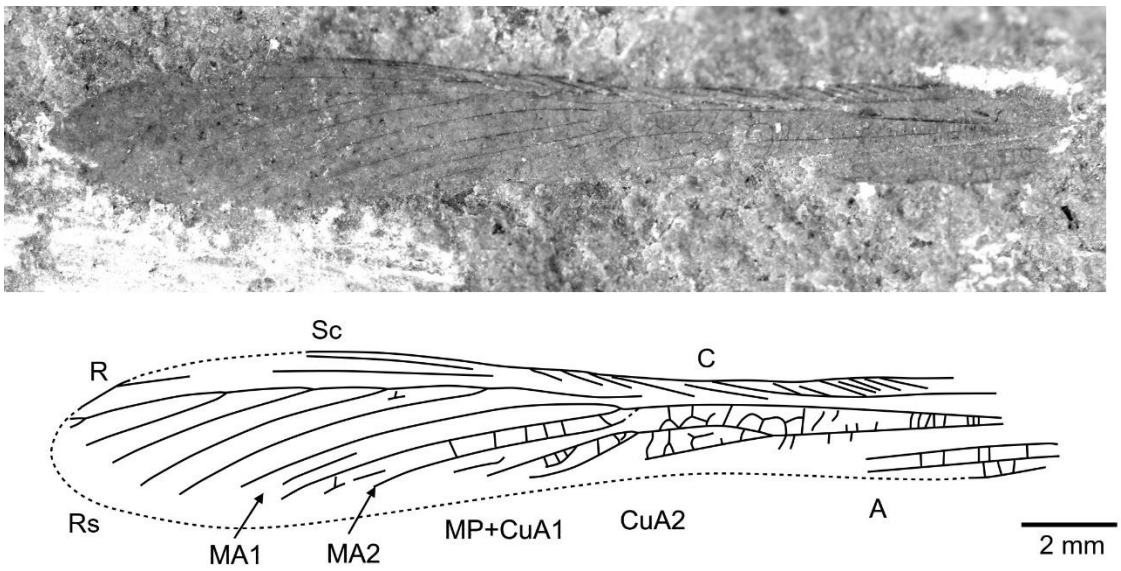

Figure 3.32. Holotype of *Locustopsis spectablis* (Zeuner, 1942) (NHMUK I.10563), for Kelly and Ross (In preparation b).

Description.—Holotype is a forewing with preserved length 25.5 mm and width 4.0 mm. Slightly contorted at anterior edge which makes tracing the anterior veins difficult. Five oblique branches of Rs (six veins reaching the margin); Rs curves towards M and some specimens show evidence of a cross-vein between Rs and M. MP+CuA1 has two branches and CuA2 simple; CuP simple. C reaches the anterior margin within one third of the length of the wing and has many oblique veins. MP+CuA1 reaches the margin at two thirds the length of the wing.

Locustopsis ornatum (Whalley, 1985)

1985 *Orichalcum ornatum* Whalley, pp. 129–130, figs 16, 21.

1993 *Orichalcum ornatum* Whalley; Ross and Jarzembowski, p. 379.

2010 *Orichalcum ornatum* Whalley; Jarzembowski and Palmer, p. 174.

2015 *Orichalcum ornatum* Whalley; Nicholson et al., Suppl., p. 71.

Holotype.—NHMUK In.53983 (Fig. 3.33) ‘flatstones’ (Bed 83) of the Obtusum Zone: Obtusum Subzone (Lias Group: Charmouth Mudstone Formation: Black Ven Mudstone Member); Early Jurassic: Upper Sinemurian; Black Ven, Dorset.

Additional material.—NHMUK: In.59357, In.49208, In.49593 and In.53917 Black Ven, Charmouth (Sinemurian).

Emended diagnosis.—Similar size to *L. spectablis* (length c. 21–29 mm) but with highly patterned wings; Rs is unique, with three oblique branches of Rs running posteriorly and two running anteriorly; stalk of Rs runs very close to anterior branch of MA1.

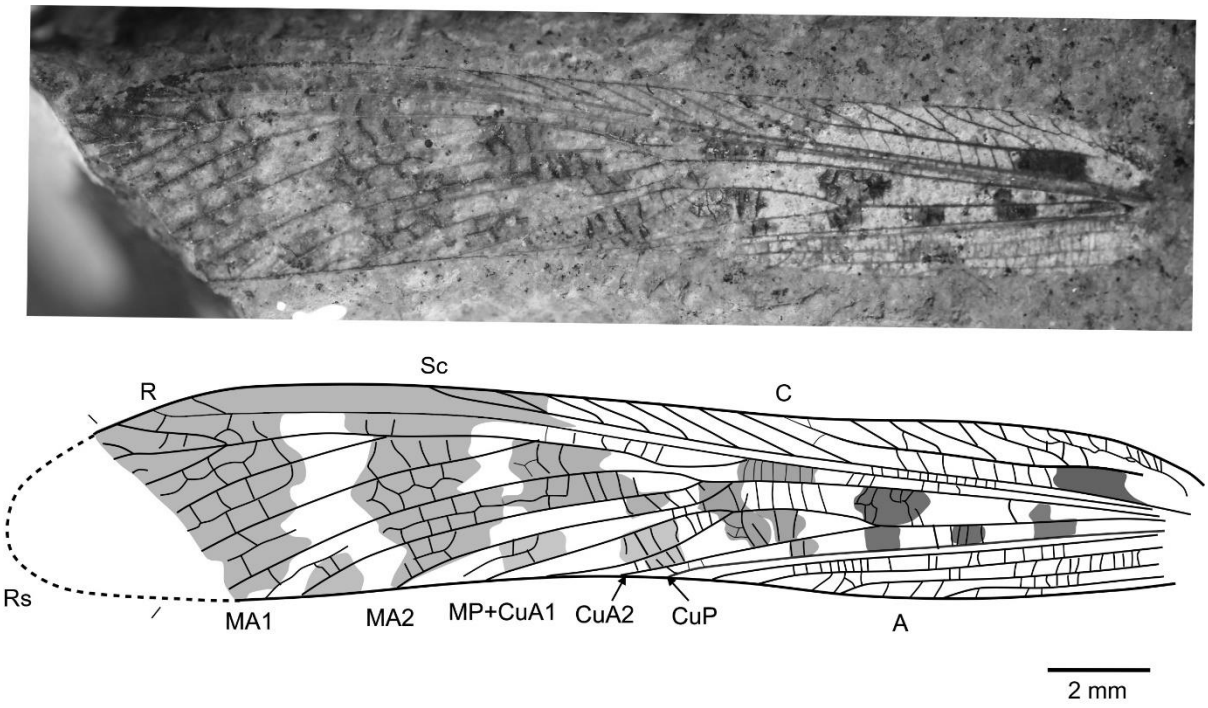

Figure 3.33. Holotype of *Locustopsis ornatum* (Whalley, 1985) (NHMUK In.53983), for Kelly and Ross (In preparation b).

Description.—Holotype is a forewing, length 26 mm, width 4.5 mm. C meets the anterior margin one third along the wing length and Sc at two thirds the length, both have oblique branches to the margin

(C has 8, Sc has 9). R runs almost to apex with anterior branch near tip; Rs leaves R at approximately mid-wing, three oblique veins run posteriorly and two anteriorly; M is typical for the genus with a bifurcated MA1 and a simple MA2. Bifurcated MP+CuA1 terminating just before two thirds the length *Remarks.*—This species is very similar to *L. spectablis* but is younger, only being found in Sinemurian deposits, and is much more heavily pigmented.

"Orth:Loc. sp. nov."

Holotype.—NHMUK 51043 (Fig. 3.34), 'flatstones' (bed 83) of the Obtusum Zone: Obtusum Subzone (Lias Group: Charmouth Mudstone Formation: Black Ven Mudstone Member); Early Jurassic: Upper Sinemurian; Black Ven, Dorset.

Diagnosis.—Holotype, forewing preserved length 24.5 mm, width 4.3 mm. Rs with five branches, small fork at apical end and one oblique vein further bifurcated. Three branches of MP+CuA1 with posterior branch bifurcated.

Description.—C not preserved. Sc with 10 oblique anterior branches. Rs bifurcates into four branches at tip, then with three posterior oblique branches. MA1 bifurcates, MA2 simple. MP+CuA1 simple, CuA2 bifurcates. CuP simple. There are clearly dark coloured spots basally and more solid colour apically, but it is unclear where the transition occurs as membrane preservation is patchy towards the middle of the wing.

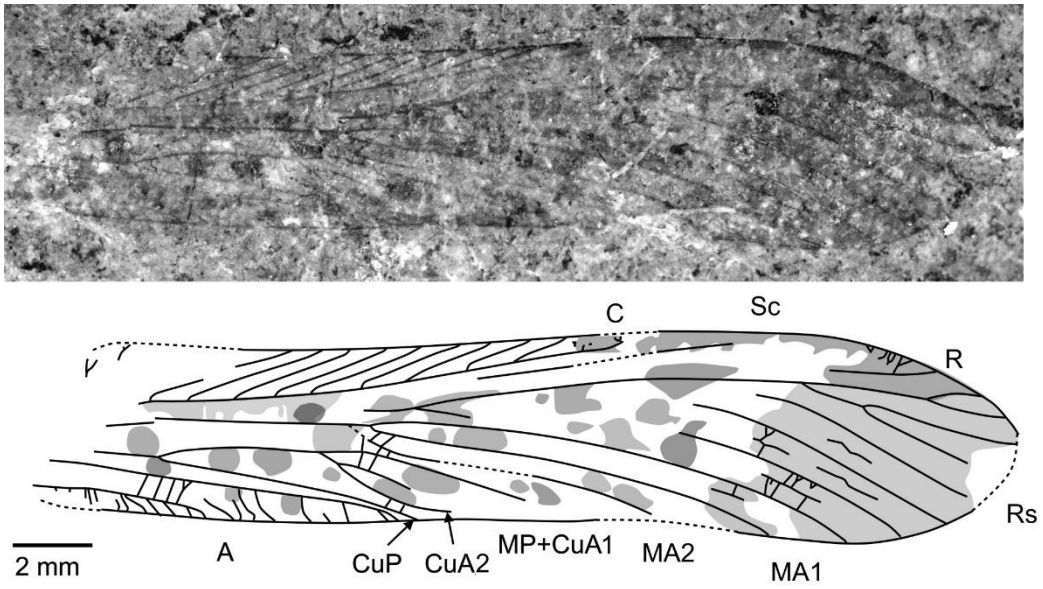

Figure 3.34. Holotype of "Orth:Loc. sp. nov." (NHMUK 51043), figure prepared for Kelly and Ross (In preparation b).

Mesolocustopsis Hong and Wang, 1990

Type species.—*Mesolocustopsis sinica* Hong and Wang, 1990.

Diagnosis.—Forewing characters as in Gorochov et al. (2006): three branches of MA with position of posterior branch of MA1 primitive as in *Locustopsis*; single branch of MP+CuA1.

Remarks.—This genus may be a junior synonym of *Locustopsis*, see Remarks section of *Locustopsis* above. *Mesolocustopsis* was described from the Lower Cretaceous of China (Hong and Wang, 1990) but Gorochov et al. (2006) included *Locustopsis dobbertinensis* and *L. magnifica* from the Lower Jurassic of Germany extending the genus back to at least the Toarcian. The English species extend it further back to the Late Triassic.

Mesolocustopsis constricta (Zeuner, 1942)

1942 *Locustopsis constricta* Zeuner, p. 12, fig. 5.
1983 *Locustopsis constricta* Zeuner; Zessin, p. 183, fig. 9.
1991 *Locustopsis constricta* Zeuner; Zessin, table 1.
1998 *Locustopsis constricta* Zeuner; Martins-Neto, p. 134, fig. 1.

Holotype.—NHMUK I.10545 (Fig. 3.35) Insect limestone/*Pseudomonotis* bed (Lilstock Formation: Cotham Member); Late Triassic: upper Rhaetian; Strensham, Worcestershire.

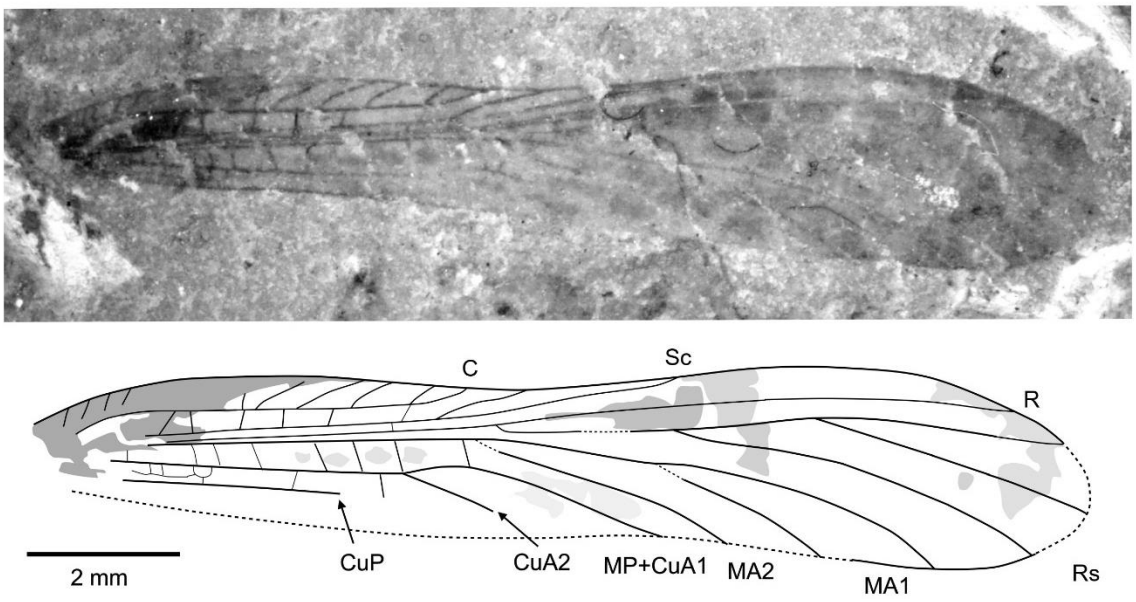

Figure 3.35. Holotype of *Mesolocustopsis constricta* (Zeuner, 1942) (NHMUK I.10545), for Kelly and Ross (In preparation b).

Diagnosis.—Forewing characters: length c. 14 mm; anterior margin is convex, creating a 'constriction' in the middle of the wing; combination of branching Sc, three or four branches of Rs, stalk of MA long.

Description.—Holotype is a forewing, length 13.7 mm, width 2.5 mm. Costal region strongly pigmented with five anterior oblique branches of C, of which the first two merge. Sc bifurcates just before termination of C. Rs with four branches, originates in the middle of the wing. MA1+2 branches at around two thirds of the length of wing. MP+CuA1 terminates just beyond the middle of the wing. CuP faint and simple. One faint anal vein. Pigmented at base of wing and patchy pigmentation in distal half.

Mesolocustopsis gracilis (Zeuner, 1942)

1983 *Locustopsis gracilis* Zeuner; Zessin, p. 183, fig. 8.

Holotype.—NHMUK I.10555 (Fig. 3.36) Insect limestone/*Pseudomonotis* bed (Lilstock Formation: Cotham Member); Late Triassic: upper Rhaetian; Strensham, Worcestershire.

Diagnosis.—Mesolocustopsis with combination of: Sc with five branches; R with three branches and stalk of MA much shorter than in *M. constricta*.

Description.—Forewing holotype, length 14.4 mm, width 2.5 mm.

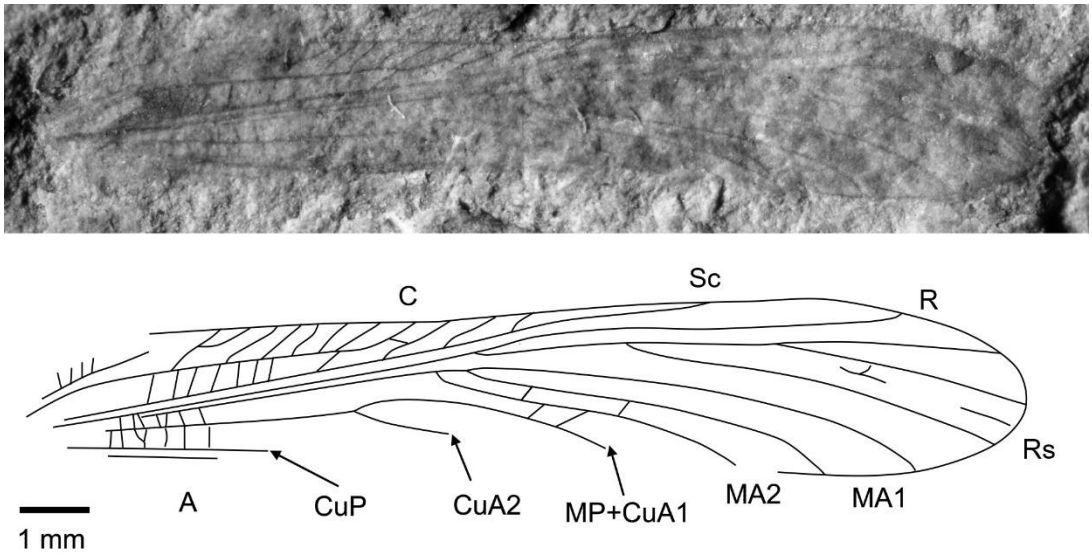

Figure 3.36. Holotype of *Mesolocustopsis gracilis* (Zeuner, 1942) (NHMUK I.10555), for Kelly and Ross (In preparation b).

Locustopsis cockerelli Handlirsch, 1939 *nomen dubium*

1939 *Locustopsis cockerelli* Handlirsch, p. 34.

1942 *Locustopsis cockerelli* Handlirsch; Zeuner, p. 9.

1983 *Locustopsis cockerelli* Handlirsch; Zessin, p. 182.

Holotype.—USNM 61391 (Lacoe number 3461) (Fig. 3.37), Planorbis Zone (Lias Group: Blue Lias Formation: Wilmcote Limestone Member); Early Jurassic: Lower Hettangian; Binton, Warwickshire.

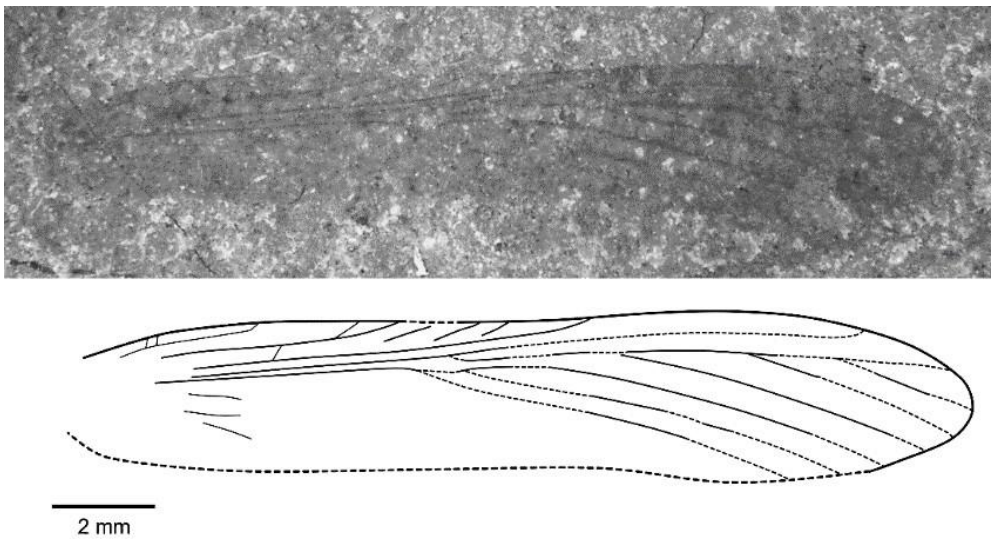

Figure 3.37. Holotype of *Locustopsis cockerelli* Handlirsch, 1939 *nomen dubium* (USNM 61391, Lacoe number 3461), for Kelly and Ross (In preparation b).

Description.—The specimen is a forewing, length 19 mm; three oblique branches of Rs; Cu not preserved.

Remarks.—One of the Lacoe specimens was identified as *L. bucklandi* by Cockerell (1915) but was then re-interpreted as the new species *L. cockerelli* Handlirsch, 1939. No description or figure, however, was given with this decision. Similarly, Cockerell did not provide a figure. The specimen is not well preserved and some key areas for characterising species, such as Cu, are not visible, it is therefore unclear what Handlirsch saw to erect a new species. The specimen is too poorly preserved to decide if it constitutes a species in its own right or should be synonymised therefore, we regard it as *nomen dubium.*

ORTHOPTERA *incertae sedis*

‘*Gryllus*’ *bucklandi* Brodie, 1845 *nomen dubium*

1845 *Gryllus bucklandi* Brodie, pp. 76, 96, 101; pl. 7, fig. 16. *nomen dubium*
1856 *Oedipoda bucklandi* (Brodie); Giebel, p. 309.
1872 *Gryllus bucklandi* Brodie; Phillips, p. 123.
1891 *Gryllus bucklandi* Brodie; Scudder, p. 118, no. 720.
1891 *Oedipoda bucklandi* (Brodie); Scudder, p. 123, no. 764.
1906 ? *Locustopsis bucklandi* (Brodie); Handlirsch, p. 422.
1915 *Locustopsis bucklandi* (Brodie); Cockerell, p. 473.
1939 *Locustopsis bucklandi* (Brodie); Handlirsch, p. 34.
1968 *Locustopsis bucklandi* (Brodie); Sharov, p. 92.
1983 *Locustopsis bucklandi* (Brodie); Zessin, p. 186, fig. 12.
2016 *Locustopsis bucklandi* (Brodie); Gu et al., p. 379.

Holotype.—NHMUK I.3555 (Fig. 3.38), Planorbis Zone (Lias Group: Blue Lias Formation: Wilmcote Limestone Member); Early Jurassic: Lower Hettangian; Temple Grafton, Warwickshire.

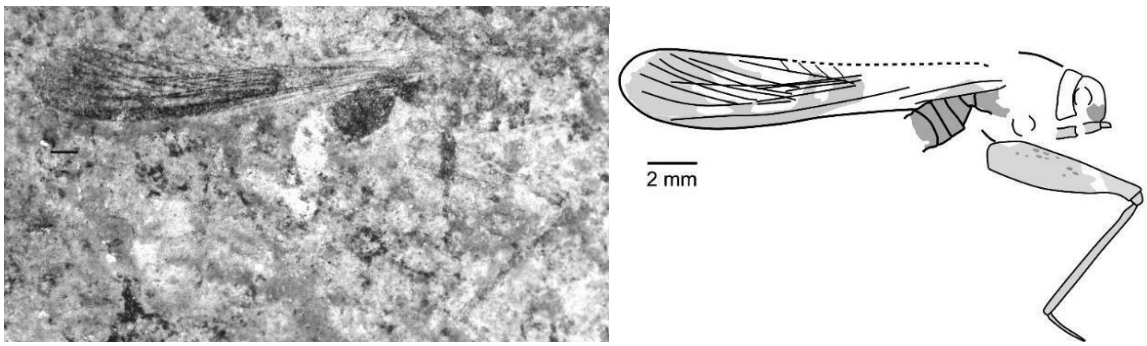

Figure 3.38. Holotype of '*Gryllus*' *bucklandi* Brodie, 1845 *nomen dubium* (NHMUK I.3555), for Kelly and Ross (In preparation b).

Remarks.—The specimen was originally figured by Brodie (1845), but the venation is inaccurate and although Giebel (1856) and Handlirsch (1906–08) discussed the specimen they did not examine the holotype or provide further figures. The holotype was examined by Zeuner (1942) who provided a composite figure of the holotype and NHMUK I.10450, this was subsequently redrawn by Zessin (1983) without examination of the Holotype.—After careful examination of the holotype and all specimens identified as this species it is not at all clear whether it represents a distinct species or even which genus it belongs to, it may not even belong to the Locustopseidae as the wing and leg may also be similar to the ensiferan family Elcanidae (e.g. see holotype for *Panorpidium yixianensis* Fang et al., 2015, fig. 3 or Grimaldi and Engel, 2005, p. 208, fig. 7.29). This is still an important specimen as it is one of the only British orthopterans to preserve body parts other than wings, but unfortunately the venation is not clear enough for taxonomic assignment.

Palaeotermes ellisii Woodward, 1892 *nomen dubium*

1892 *Palaeotermes ellisii* Woodward: 198, pl. 5, fig. 1.
1893 *Palaeotermes ellisii* Woodward; Woodward: 168, 367.
1893 *Palaeotermes ellisii* Woodward; Cope and Kingsley: 150.
1939 *Palaeotermes Ellisii* Woodward; Handlirsch: 149.

Holotype.—NHMUK I.2348 (pt), LEICT G572.1889 (cpt) (Fig. 3.39). Planorbis Zone, Blue Lias Formation; Lower Lias: Hettangian; Barrow–on–Soar, Leicestershire.

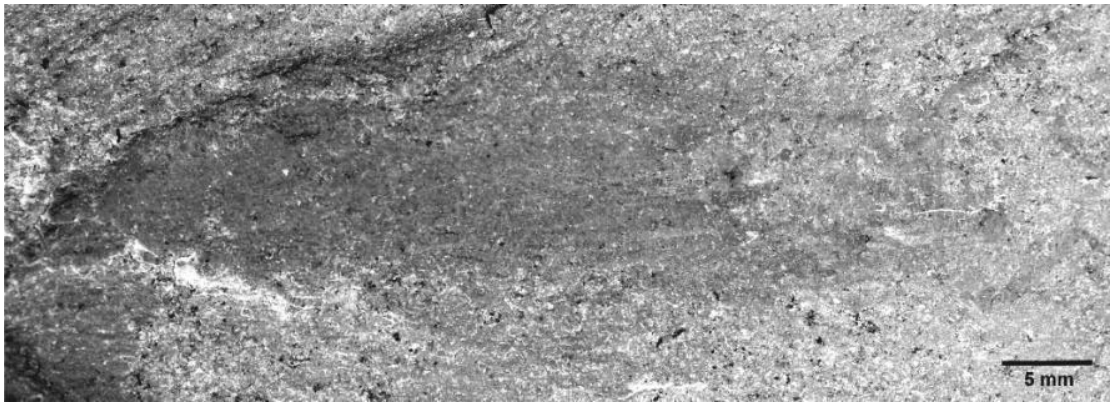

Figure 3.39. Holotype of *Palaeotermes ellisii* Woodward, 1892 *nomen dubium* (NHMUK I.2348), for Kelly and Ross (In preparation d).

Remarks.—This is a very poorly preserved specimen with very faint venation and possible remnants of head and legs. The original figure (Woodward, 1892, pl. 5, fig. 1) is not entirely accurate to the state of the specimen today and many of the characters originally indicated are not evident, even when

examined under alcohol. The wings are folded so clearly a neopteran and the general habitus is consistent with Orthoptera. It may be a bintoniellid however the specimen is too poorly preserved and the venation too incomplete to confirm, thus we consider this taxon to be *nomen dubium*.

Conclusions.—The type genus of the cricket family Bintoniellidae, *Bintoniella* Handlirsch, 1939, is considered a junior synonym of *Haglopsis* Handlirsch, 1906. *Bintoniella brodiei* Handlirsch, 1939 and *Orthophlebia longissima* Giebel, 1856 are considered junior synonyms of *Haglopsis parallela* (Giebel, 1856), *Haglopsis brodiei* Cockerell, 1915 remains a separate species. *Palaeotermes ellisii* Woodward, 1892 is considered *nomen dubium*. The holotype of the type genus of the grasshopper family Locustopseidae, *Locustopsis elegans* Handlirsch, 1907, was re-examined for the first time since its original description (Handlirsch, 1907), which was found to be inaccurate. The venation is unclear and as such *Mesolocustopsis* Hong and Wang, 1990 may be a junior synonym of *Locustopsis* Handlirsch, 1907 but there is not enough evidence to synonymise them. *Locustopsis lacoei* Cockerell, 1915, *Locustopsis spectablis* Zeuner, 1942, and *Locustopsis ornatum* (Whalley, 1985), therefore, are retained in *Locustopsis*, "Orth:Loc. sp. nov." is described from the Jackson collection and *L. constricta* and *L. gracilis* are transferred to *Mesolocustopsis*. *Locustopsis cockerelli* Handlirsch, 1939 and *Locustopsis bucklandi* (Brodie, 1845) are considered *nomen dubia*.

The cricket genus *Archelcana* (Elcanidae) is redescribed based on changes to the family made by Gorochov et al. (2006). *Archelcana liasina* (Giebel, 1856) and *Archelcana geinitzi* (Heer, 1880) are transferred to this genus and *A. liasina* is the senior synonym of *Archelcana durnovaria* Whalley, 1985, *Elcana signata* (Heer, 1865) and *Elcana maculata* (Heer, 1865). "Orth:Elc. sp. nov." is described from the Brodie collection. The holotype for *Elcana obtecta* (Heer, 1865) is considered lost and *Elcana troglodytes* (Heer, 1865) is considered *nomen dubium*. "Orth:Hag. gen. et sp." is described in the cricket family Haglidae.

3.3.4 Phasmatodea

There is one specimen of stick-insect known from the Sinemurian of Dorset (Whalley, 1985), described as Aerophasmatidae: *Durnovaria parallela* (Fig. 3.40). A search through the collections at all museums visited did not turn up any further specimens. There is very little literature on this species, but the taxonomy of the species is generally agreed (Ansorge, 1996, 2003; Nel et al., 2004). There was a similar specimen found in the Toarcian of Grimmen, Germany and assigned as *Durnovaria* cf. *parallela* (Ansorge, 1996) and *Durnovaria parallela* (Ansorge 2003). (Wang and Ren, 2013) list *D. parallela* as coming from "T2; T3" of England suggesting that the family crosses the TJB. This is not the case and the species is only known from the Sinemurian (J1) of England meaning that it is not known before the TJB as reported in Nicholson et al. (2015). The closely related *Aeroplana* is known

from before the TJB and has only been found in the Carnian Blackstone Formation of Australia (Tillyard, 1918; Jell, 2004).

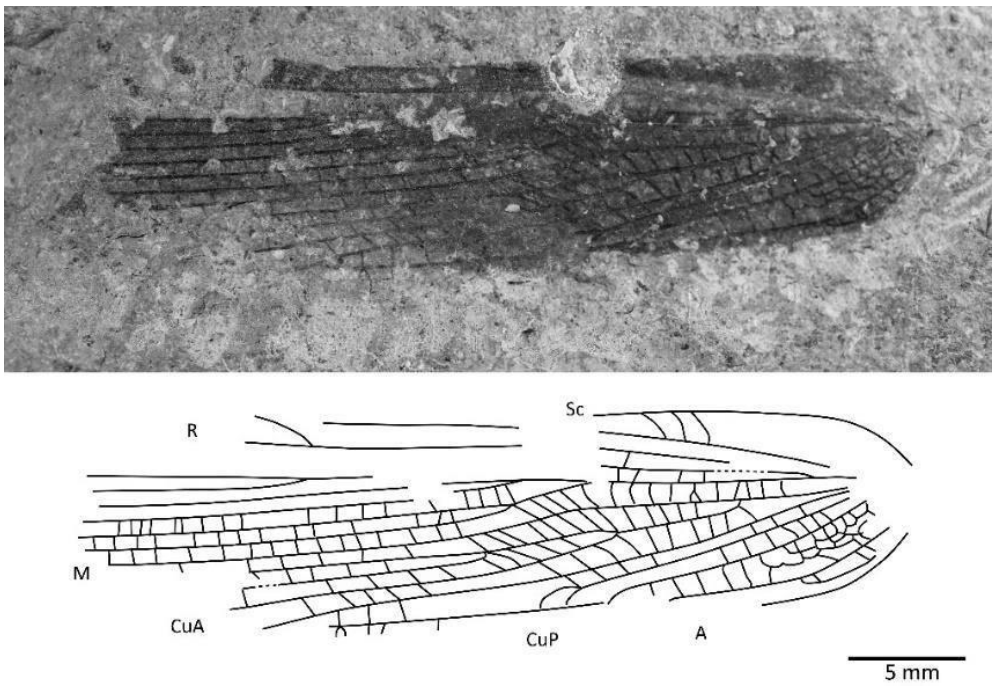

Figure 3.40. Holotype of *Durnovaria parallela* Whalley, 1985 (NHMUK In.59171).

3.3.5 Hemiptera

The bugs (Hemiptera) are the most successful of the hemimetabolous orders in terms of species diversity and biogeography (Grimaldi and Engel, 2005) (Fig. 3.41). There are six proposed monophyletic suborders: Heteroptera ('true-bugs'), Sternorrhyncha (aphids, whiteflies and scale insects), Coleorrhyncha (moss bugs), Cicadomorpha (cicadas, leafhoppers, treehoppers and spittlebugs), Fulgoromorpha (planthoppers) and Palaeorrhyncha (primitive bugs) which share a unique structure of segmented rostrum adapted for sucking as the main synapomorphic character. The term 'Homoptera' was previously used to refer to the paraphyletic grouping of the non-heteropteran suborders but has since been abandoned. Cicadomorpha and Fulgoromorpha were originally grouped together as the suborder Auchenorrhyncha, but this was considered a paraphyletic grouping and split into the most probable monophyletic clades (Szwedo et al., 2004). Although still disputed by a range of evidence (Cryan and Urban, 2012) this classification is still considered valid (Szwedo, 2018). The Heteroptera and Coleorrhyncha were revised relatively recently (Popov et al., 1994) and there are no Palaeorrhyncha known from the Triassic/Jurassic of Britain, so the focus of the revisions herein was on the auchenorrhynchan suborders: Cicadomorpha and Fulgoromorpha.

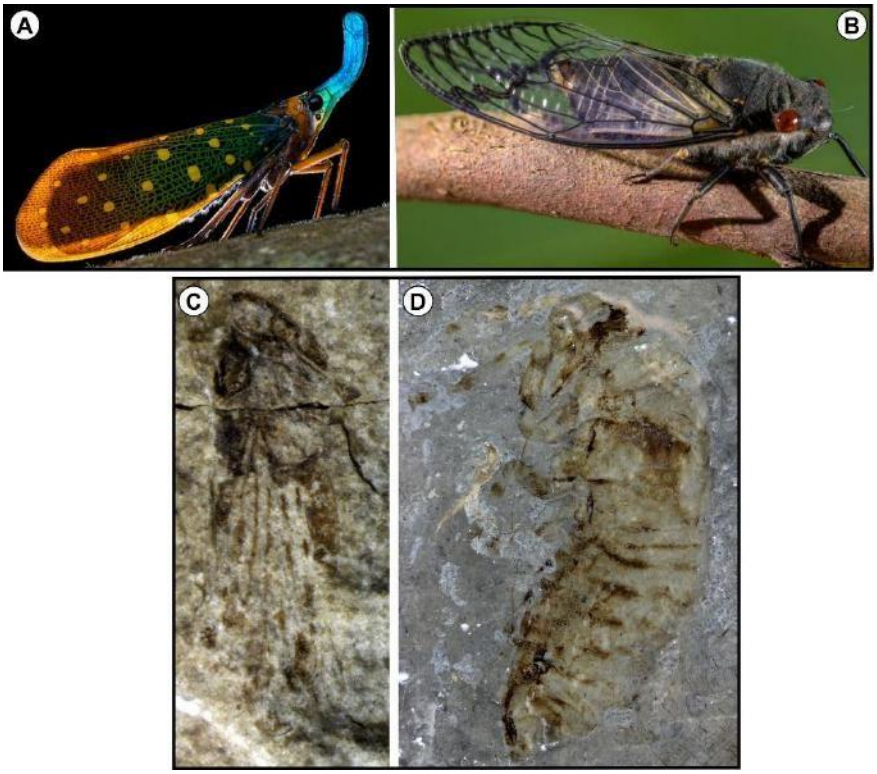

Figure 3.41. Examples of bugs of the suborders Hemiptera: Fulogoromorpha and Cicadomorpha. A. Extant lanternbug (planthopper), Fulgoridae, *Pyrops whiteheadi* (photo by Nicky Bay), B. Extant cicada, *Magicicada* sp. (photo by Nathan Emery), C. Jurassic planthopper, *Margaroptilon* sp. (NHMUK I.3079), D. Triassic cicada, '*Liassocicada' ignotatus* (NHMUK I.11240).

The first accounts of Mesozoic auchenorrhynchans from Britain were published by Brodie (1845) from latest Triassic and Early Jurassic deposits. Species described were *Asilius* (?) *ignotatus* Brodie, 1845 (originally Diptera), *Cicada murchisoni* Brodie, 1845 and two specimens: "Cicada larva" and "Cicada pupa". Further species were described based on Brodie's material: *Margaroptilon brodiei* Handlirsch, 1906, *M. woodwardi* Handlirsch, 1906 and *M. bulleni* Handlirsch, 1906, also *Belostoma liasina* Giebel, 1856 was transferred to *Dysmorphoptila* (Handlirsch, 1906). The previous cicada species from Brodie (1845) were combined into *Liassocicada ignotus* (Brodie, 1845) in Cicadidae by Whalley (1985); Carpenter (1992) considered these specimens too poorly preserved for familial placement but they were not formally removed until (Shcherbakov, 2009), who considered them to belong to Tettigarctidae. Other species described by Whalley (1985) were *Paraprosbole rotruda* Whalley, 1985, which was later moved to *Shuraboprosbole* by Chen et al. (2016), and *Mesocixiella* (?) *fennahi* Whalley, 1985.

Systematic Palaeontology

Order HEMIPTERA Linnaéus, 1758

Superfamily CERCOPOIDEA Westwood, 1838

Family PROCERCOPIDAE Handlirsch, 1906

Genus PROCERCOPIS Handlirsch, 1906

"Hem:Proc. sp. nov. 1"

Holotype.—NHMUK I.10593/I.10876 (pt and cpt) (Fig. 3.42), Penarth Group: upper Rhaetian: Lilstock Formation: Langport Member of Brown's Wood, Warwickshire.

Paratypes.—Rhaetian: NHMUK I.10626/I.11039 (pt and cpt) and I.10877/I.10898 (pt and cpt) both from Brown's Wood.

Additional material.—Rhaetian: NHMUK I.10605, I.10908, I.10904/I.10908 (pt and cpt), and I.10893 Brown's Wood; I.11751 locality unknown.

Diagnosis.—*Procercopis* tegmen (forewing), length c. 11.5 mm, width 2.5 mm with the following combination of characters: main medial fork distal of R; only one r-m crossvein; MP simple.

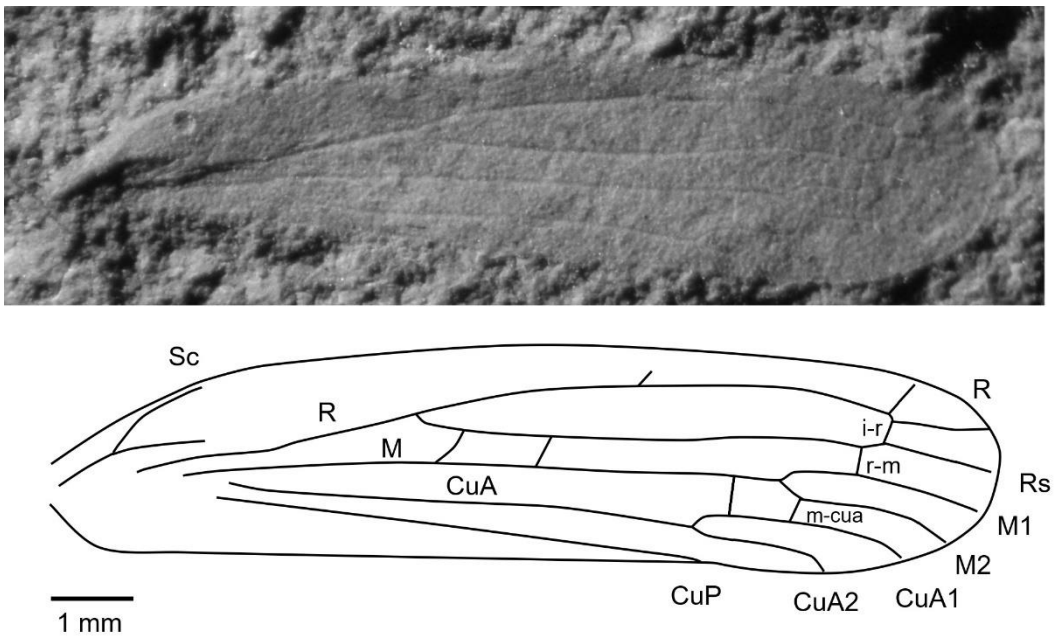

Figure 3.42. Holotype of "Hem:Proc. sp. nov. 1" (NHMUK I.10593/I.10876), for Kelly et al. (In preparation b).

Description.—Holotype is a forewing, length 11.5 mm, width 2.7 mm at its widest point. R and Rs split just after one third of the length of the wing, connected by a single cross-vein near the apex; M straight, splits into MA and MP at three quarters of the length of wing; CuA straight, bifurcates at two thirds the length of wing, connected to MP by a cross-vein; CuP straight and simple, terminates on posterior margin at two thirds of the length of the wing. Although the paratypes are not as well preserved or incomplete they can be regarded as conspecific from their similar size and discernible venation.

Remarks.—There are 13 other species recorded in this genus, one from the Late Triassic of Kyrgyzstan: *P. longipennis* Becker-Migdisova, 1962; one from the Lower Jurassic of China: *P. shawanensis* Zhang et al., 2003 and 11 from the Lower Jurassic: Upper Lias of Germany: *P. jurassica* (Geinitz, 1884); *P. alutacea* Handlirsch, 1906; *P. liasina* Handlirsch, 1906; *P. coriacea* Handlirsch, 1939; *P. similis* Handlirsch, 1939; *P. abscissa* Bode, 1953; *P. completa* Bode, 1953; *P. debilis* Bode, 1953; *P. lacerate* Bode, 1953, *P. wunnenbergi* Bode, 1953 and *P. frenzeli* Ansorge, 1996.

Most of the Handlirsch species were revised but most were not refigured (Evans, 1956). Based on the available published figures: *P. jurassica* (Handlirsch, 1906, pl. 43, fig. 39; Evans, 1956, fig. 16E), *P. liasina* (Handlirsch, 1906, pl. 43, fig. 40) and *P. similis* (Handlirsch, 1939, pl. 15, fig. 291) are based on hindwings so are impossible to compare with the current species which is based on a forewing. *P. alutacea* (Handlirsch, 1906, pl. 43, fig. 38) and *P. coriacea* (Handlirsch, 1939, pl. 15, fig. 285) are based on forewings. In *P. alutacea* Sc is not forked, there are more crossveins in the apical section and there is an additional vein in the medial system and *P. coriacea* only preserves the apical region and so is difficult to compare but there are a lot more crossveins than seen in the holotype of the current species. These species are, however, in need of revision.

The Bode species have not been revised since their description and only Bode's figures have been published. It is difficult to work solely from historical figures of holotypes but based on the figures in Bode (1953) *P. abscissa* (pl. 10, fig. 206), *P. debilis* (pl. 10, fig. 207), *P. completa* (pl. 10, fig. 208), and possibly *P. lacerate* (pl. 10, fig. 209) are also based on hindwings. *P. wunnenbergi* (pl. 10, fig. 205) is based on a forewing but it displays quite a developed precostal region which is not present in other species of *Procercopis*. The Bode collection in Germany needs revision to properly ascertain whether the taxonomy proposed by Bode stands up to modern scrutiny.

The holotype for *P. longipennis* Becker-Migdisova, 1962 was examined at PIN, the medial fork is much deeper in *P. longipennis* occurring approximately in line with R1; whereas in *the* new species this fork is quite distal to R1, the character is not preserved in *P. shawnaensis* and R1 is not preserved in *P. frenzeli*. In *P. longipennis* there is an additional r-m crossvein forming a small cell in-between R

and M not seen in the other species. M_2 bifurcates twice in *P. longipennis* and *P. shawanensis*, once in *P. frenzeli* and is simple in the new species.

"Hem:Proc. sp. nov. 2"

Holotype.—NHMUK I.10610 (Fig. 3.43). Penarth Group: upper Rhaetian: Lilstock Formation: Langport Member of Brown's Wood, Warwickshire.

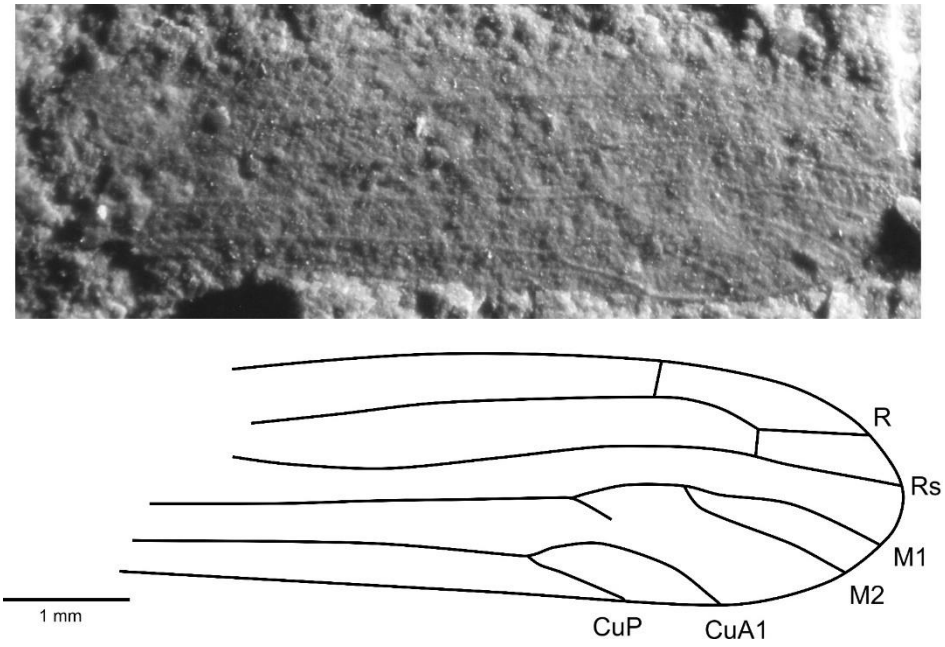

Figure 3.43. Holotype of "Hem:Proc. sp. nov. 2" (NHMUK I.10610), for Kelly et al. (In preparation b).

Diagnosis.—MP bifurcates and is connected to MA by a cross-vein.

Description.—Holotype forewing, only apical portion preserved. Preserved length 4.7 mm, width 2.3 mm.

Remarks.—Very similar to "Hem:Proc. sp. nov. 1" but has an extra bifurcation of the MA vein.

Suborder FULGOROMORPHA Evans, 1946

Superfamily FULGOROIDEA Latreille, 1807

Family FULGORIDIIDAE Handlirsch, 1939

Genus MARGAROPTILON Handlirsch, 1908

Margaroptilon woodwardi Handlirsch, 1908

1908 *Margaroptilon brodiei* Handlirsch, p. 499.

1908 *Margaroptilon woodwardi* Handlirsch, p. 499, pl. 43, fig. 35.

1908 *Margaroptilon bulleni*, Handlirsch, p. 499, pl. 43, fig. 36.

2004 *Margaroptilon brodiei* Handlirsch; Szwedo et al., p. 69.

2004 *Margaroptilon woodwardi* Handlirsch; Szwedo et al., p. 70.

2004 *Margaroptilon bulleni*, Handlirsch; Szwedo et al., p. 69.

Holotype.—NHMUK I.11286/I.11266 (Fig. 3.44), 'Fish and insect beds' of the Falciferum Zone (Lias Group: Whitby Mudstone Formation: Jet Rock Member); Early Jurassic: Lower Toarcian; Alderton, Gloucestershire.

Additional material.—Toarcian: NHMUK I.3561 (Brodie, 1845, pl. 8, fig. 10) (Fig. 3.45), 11296 (pt and cpt), I.3341 and CHAGM F.659 from Alderton quarry; NHMUK I.15015, I.11429, I.3309, I.11399, I.11426, I.11374, I.11414 and CHAGM F.635, F.642, F.661 and F.664 from Dumbleton quarry; NHMUK I.11492 and NMW 39/2011/0593 from Ilminster.

Diagnosis.—Small wings, length c. 7 mm, width c. 3 mm with distinct maculations throughout.

Description.—Holotype 7.1 mm long, width 2.9 mm. I.3309 width 3.1 mm

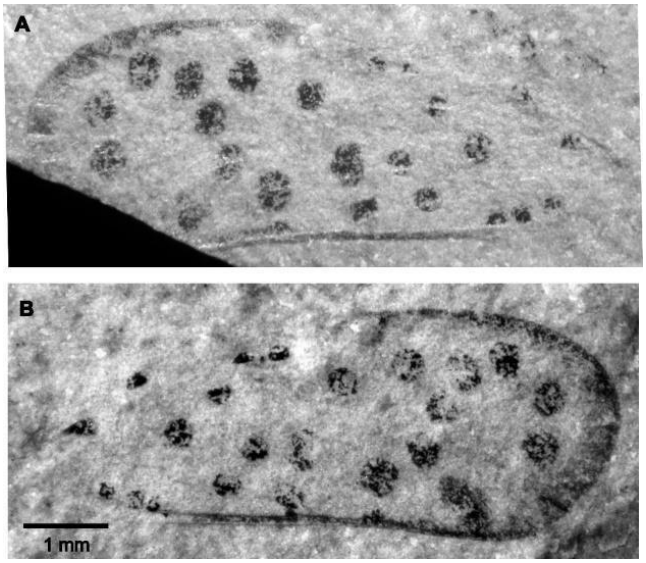

Figure 3.44. Holotype of *Margaroptilon woodwardi* Handlirsch, 1908, A. NHMUK I.11286, B. NHMUK I.11266, holotype of *M. bulleni*, for Kelly et al. (In preparation b).

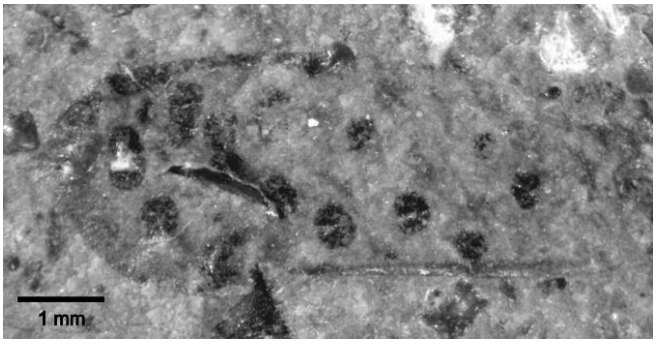

Figure 3.45. *Margaroptilon woodwardi*, holotype of *M. brodiei* Handlirsch, 1908 (NHMUK I.3561), for Kelly et al. (In preparation b).

Remarks.—Three specimens were described as three different species by Handlirsch (1908) but there is no evidence to suggest that they are different species (two of them are part and counterpart of the same specimen). All three species were described based on slight variation in configuration of the dark spots which could easily be explained by intraspecific variation or diagenetic process. The extremely poor preservation of these three specimens leaves little confidence in their affinities but they are generally similar, they are of a similar size, shape and have maculations throughout the wing. They are also all from the same locality (Alderton/Dumbleton, Gloucestershire) except one which is from the same aged horizon in Ilminster, Somerset. Thus, we regard these specimens as conspecific and update the diagnosis of the senior synonym *Margaroptilon brodiei* accordingly.

Conclusions.—Two new species were described in the froghopper genus *Procercopis*, "Hem:Proc. sp. nov. 1" and "Hem:Proc. sp. nov. 2." Three planthopper species were synonymised based on morphological similarity, *Margaroptilon brodiei* Handlirsch, 1908; *Margaroptilon bulleni* Handlirsch (1908), and *Margaroptilon woodwardi* Handlirsch, 1908, the latter being the senior synonym.

3.3.6 Coleoptera

This order contains the beetles, an incredibly diverse order of insects with forewings hardened into elytra as their main characteristic trait (Gullan and Cranston, 2010) (Fig. 3.46). There are several families of beetles described from the British Late Triassic and Early Jurassic, many of which are still extant, e.g.: Buprestidae (jewel beetles), Elateridae (click beetles), Chrysomelidae (leaf beetles) and Gyrinidae (whirligig beetles). The affinity of these fragmentary specimens with extant families is dubious but it is not possible to revise them without more complete material.

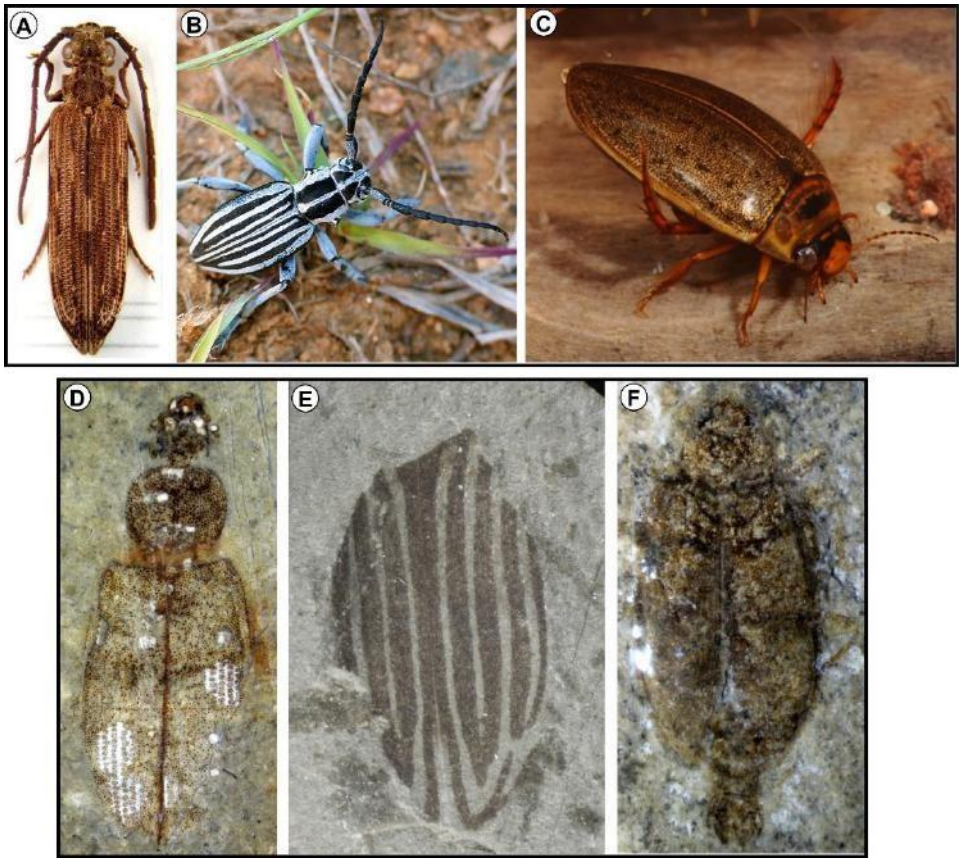

Figure 3.46. Examples of beetles of the order Coleoptera. A. Extant Cupedidae, *Cupes anguliscutus* (photo by K.V. Makarov), B. Extant Cerambycidae, *Dorcadion buresi* (photo by Karei Hodek), C. Extant Dytiscidae *Rhantus suturalis* (photo by G.H. Visser), D. Triassic Cupedidae, *Liassocupes liassicum* (NHMUK I.11095), E. Jurassic Coptoclavidae, *Holcoptera giebeli* (NHMUK I.6771), F. Jurassic Dytiscidae (NHMUK I.6649).

One genus of beetles, *Holcoptera* Handlirsch, 1906, was revised for the current study as they form a large part of the Late Triassic and Early Jurassic entomofaunas of England; they are relatively simple to work with taxonomically as they exhibit a range of distinct colour patterns, which allow for specific identification, not usually preserved in beetle fossils and a new whole specimen was discovered in Dorset which allowed the genus to be assigned to the family Coptoclavidae Ponomarenko, 1961. Previously this genus was only known from elytra, so there were difficulties identifying its family. Two of Brodie's specimens (1845, pl. 6, fig. 28 and pl. 10, fig. 2) were originally named as *Harpalus schlotheimi* Giebel, 1856 before being split into *Holcoptera schlotheimi* Handlirsch, 1906 and *Holcoëlytrum giebeli* Handlirsch, 1906. The genera were synonymised by Cockerell (1915), *Holcoptera* being the senior synonym, and *H. confluens* was described from the Lacoe collection in the US. Subsequently, Zeuner (1962) mistakenly synonymised these genera giving priority to *Holcoëlytrum,* but this was corrected by Whalley (1985) who correctly stated that the original synonymisation has priority.

Systematic Palaeontology

Order COLEOPTERA Linnaeus, 1758

Family COPTOCLAVIDAE Ponomarenko, 1961

Genus HOLCOPTERA Handlirsch, 1907

Type species.—Harpalus schlotheimi Giebel, 1856

Emended diagnosis.—Elytra covering abdomen, with marked dark and light longitudinal colour bands. One of the bands is consistent in all species, being narrow and running the full length of the elytral suture. Pronotum transverse and narrower than elytra with rounded lateral edges.

Morphometric analysis.—Cockerell (1915) based his assignment of *H. confluens* on a qualitatively perceived size difference and a confluence of dark bands in the elytral colour patterning compared with *H. schlotheimi*. The differences in colour pattern remains a qualitative problem but the size difference can be assessed quantitatively and although this is not enough evidence in itself for a species assignment or synonymy, it can contribute to evidence for such an action. We therefore provide a qualitative description of all specimens as well as a statistical analysis of differences in size between species.

Given the fragmentary nature of the specimens, a full morphometric analysis was not possible, and we present a simpler method using only length and width measurements. The ‘prcomp’ command was used in the R stats package (R Core Team, 2018) to carry out a principal component analysis (PCA) on the length and width measurements forming a single variable ‘shape’. Then the GLM tool was used to apply a general linear model comparing the shapes of the three supposed species. The GLM indicates a non–significant difference in shape between *H. schlotheimi* and *H. confluens* (GLM, F = 166.89, p = 0.126) and a significant difference in shape between *H. confluens* and *H. giebeli* (GLM, F = 166.89, p = <2e–16) (Fig. 3.47). These results support a statistically significant difference in shape between *H. schlotheimi/H. confluens* and *H. giebeli* based on length and width measurements.

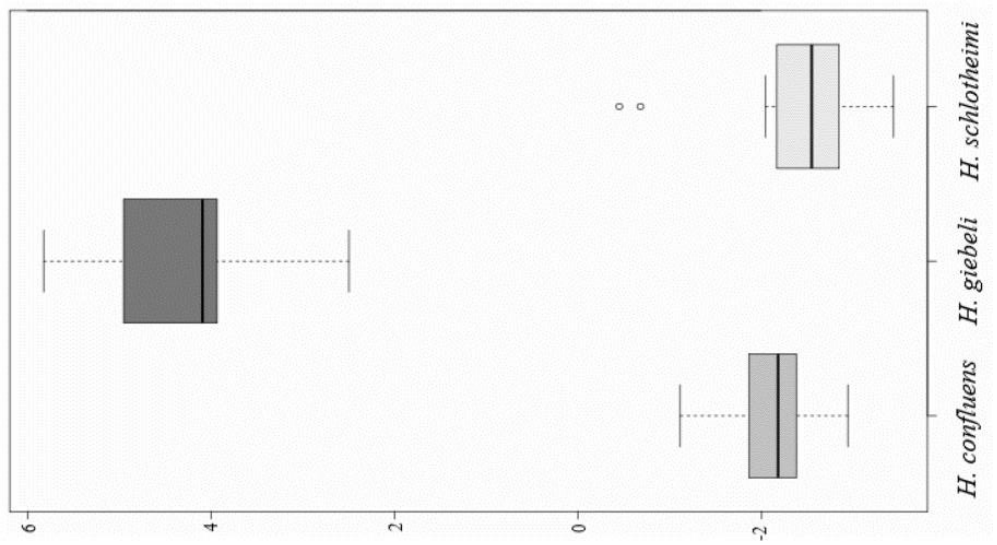

Figure 3.47. Results of GLM indicating no significant difference in shape between *H. schlotheimi* and *H. confluens* but a significant difference between both and *H. giebeli*. From Kelly et al. (2017, fig. 3), Appendix 4.

Holcoptera schlotheimi (Giebel, 1856)

1845 'Harpalideous Carabidae' Brodie, pp. 101, 124, pl. 6, fig. 28.

1856 *Harpalus Schlotheimi* Giebel, p. 63.

1891 *Harpalus schlotheimi* Giebel; Scudder, p. 210.

1907 *Holcoptera Schlotheimi* (Giebel); Handlirsch, p. 453, pl. 41, fig. 63.

1915 *Holcoptera schlotheimi* (Giebel); Cockerell, p. 480, pl. 61, fig. 7.

1915 *Holcoptera confluens* Cockerell, p. 480, pl. 61, fig. 8.

1962 *Holcoëlytrum schlotheimi* (Giebel); Zeuner, p. 170, pl. 27, fig. 5.

1985 *Holcoptera schlotheimi* (Giebel); Whalley, p. 173, fig. 82.

Holotype.—NHMUK I.10783 (Fig. 3.48), Insect limestone (Penarth Group: Lilstock Formation); upper Rhaetian; Apperley, Gloucestershire.

Additional material.—Rhaetian: NHMUK: I.4000 Apperley; I.10841 Brockeridge; I.11551 Forthampton; I.10975 Strensham. BRSMG: Cd 1387 Westbury-on-Severn; Cd 1348, YORYM: YM1983: 739F, 740F, 741F, 742F, 743F, 744F, 745F Aust Cliff. Hettangian: NHMUK: I.11007 Stratford-upon-Avon; I.10491 Wilmcote; I.3365, I.3582, I.6651, I.6653, I.6733, I.6734, I.6735, I.6737, I.6742, I.6743, I.10731, I.6786, I.11085, I.10732, I.10736, I.6682/I.11077 (pt and cpt), WARMS: G 8126: 2, 3, 4, 6, 7 Binton. Hettangian–Sinemurian: YPM: 202468, 202466, 202467, 202522, 202529, 202541, 202460, 202470, 202469, 202475, 202476, 202482, 202517, 202525, 202542, 202555, 202582, 202459, 202473, 202492, 202516, 202540, 202544, 202458, 202485, 202495, 202507, 202505, 202474, 202462, 202456, 202463, 202536, 202455, 202457, 202477, 202478, 202479,

202484, 202487, 202496, 202497, 202501, 202502, 202503, 202508, 202509, 202523, 202524, 202530, 202548, 202549, 202551, 202552. 202554, 202556, 202557, 202562, 202564, 202577, 202581, 202583, 202584, 202586 2.2 miles SE of Suffield centre, Hartford County, Connecticut, USA. Sinemurian: NMW 91.14G.137 Catherston Road (Sinemurian). Unknown: HMCZ: PALE 8709; USNM: 61406 (Lacoe 3484) (Cockerell, 1915, fig. 7), 61407 (Lacoe: 3482, 3483, 3498) (Cockerell, 1915, fig. 8) all from unknown localities in the UK.

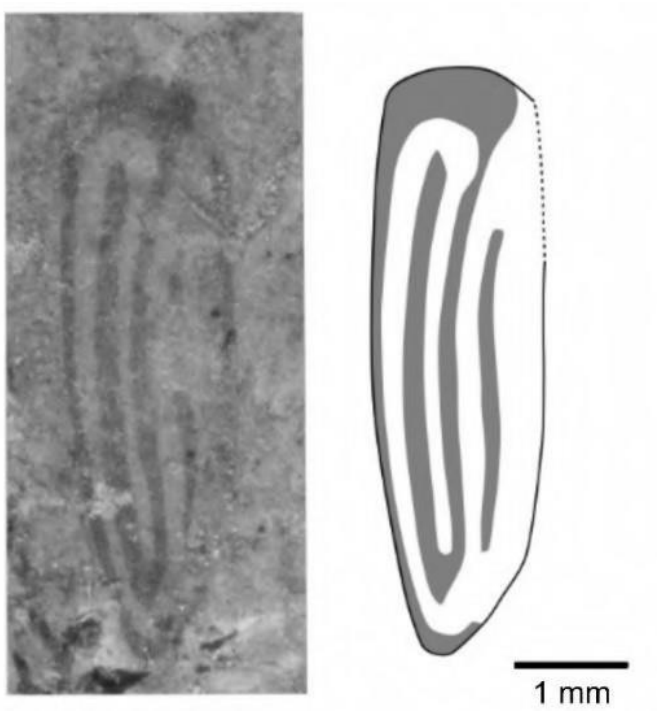

Figure 3.48. Holotype of *Holcoptera schlotheimi* (Giebel, 1856) (NHMUK I.10783), from Kelly et al. (2017, fig. 4), Appendix 4.

Emended diagnosis.—Elytra 4.8–7.5 mm long by 1.5–2.7 mm wide with variable but characteristic striped patterning. Four dark bands interspersed with four light bands, though often the darks bands are merged. The first (anterior) band is floating, i.e. not connected to other bands or to the base, the second band is connected to a dark patch at the base and the second and third bands are fused distally.

Description of holotype.—Single elytron preserved, 5.3 mm in length and 1.6 mm in width. Preservation is faint but characteristic patterning can be seen. There are four dark bands and a dark patch at the base of the elytron, the anterior band is floating, not connected to other bands or the margin, the second band is connected to the dark patch at the base and to the third band at its distal end, the third band has its base floating (not connected), the fourth band is connected to the basal dark patch and runs the full length of the elytron along the posterior margin (elytral suture). NHMUK I.11085 (Fig. 3.49A) is a complete beetle with only the legs and antennae missing. Transverse pronotum with slightly curved sides, anterior margin slightly convex. Head prognathous, slightly

bigger than pronotum. Two dorsal eyes visible. NHMUK I.6682/I.11077 (Fig. 3.49B) consists of an elytron, part of the abdomen and the hind legs. Metafemur and metatibia preserved. Metatibia slightly broadened apically but no evidence of tibial spur. Coxa and tarsi not preserved.

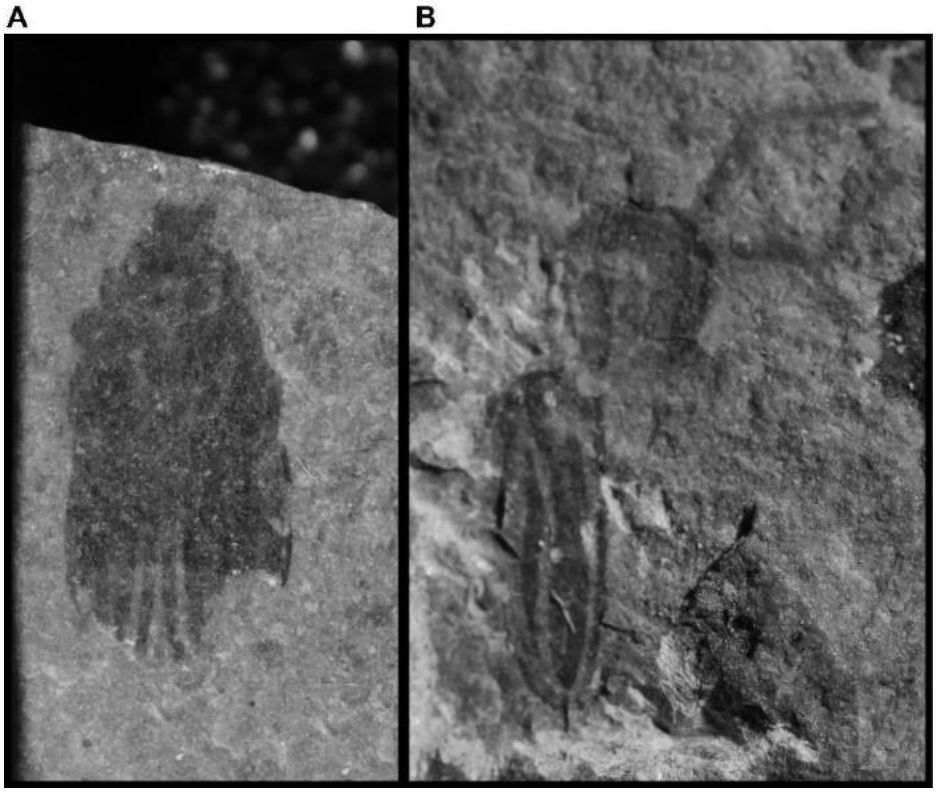

Figure 3.49. More complete examples of *H. schlotheimi*, A. NHMUK I.11085, B. NHMUK I.6682. From Kelly et al. (2017, fig. 5), Appendix 4.

Variation.—The colour pattern is highly variable, as demonstrated from a series of specimens from Binton (Fig. 3.50 A–D). The specimens are roughly the same size and given that they are from the same locality (and therefore of the same age) we consider them to be the same species rather than belonging to several species. There are varying degrees of confluence between the dark bands. Some show confluence of bands two and three along some or all of the length, sometimes forming a white hook (Fig. 3.50 B and C). Others are more heavily pigmented with confluence of bands 2–4 (Fig. 3.50 D).

Remarks.—The holotype was thought to be lost so a neotype was assigned (Zeuner, 1962). Specimen NHMUK I.10783, however, has the original figure reference of the holotype (Brodie, 1845, pl. 6, fig. 28) written on the rock in Brodie's handwriting. The neotype is rejected based on the re-discovery of the holotype, it also does not belong to this species (see below). *Holcoptera confluens* Cockerell, 1915 was named based on two characteristics, a qualitatively perceived difference in size from *H. schlotheimi*, which has been refuted by the morphometric analysis above, and a confluence of dark bands in the elytral patterning (Cockerell, 1915). The range of specimens from Binton demonstrate that this is a colour variety rather than a separate species. As previously suggested by

Zeuner (1962), differences in the relative width of the coloured bands could be caused by variable rock splitting while collecting (sometimes with wider darker bands on the counterpart and narrower on the part) and so is an artefact of the collection process rather than an indication of biological variation. This is not apparent in all specimens that have both parts and counterparts, however, so the colour variation is real.

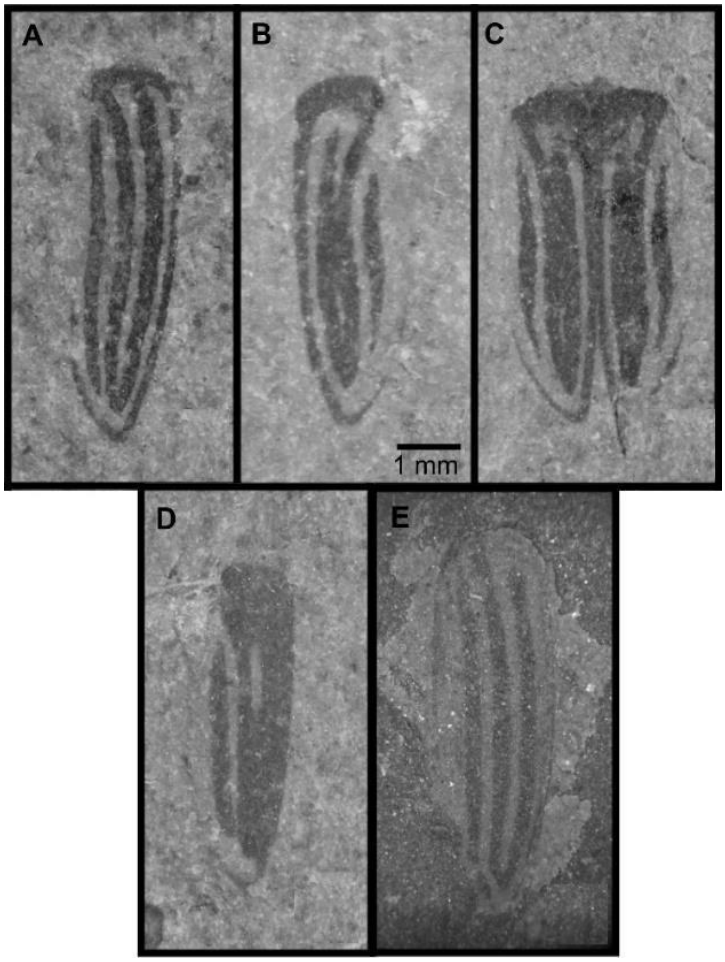

Figure 3.50. Further examples of *H. schlotheimi* showing variation in banding, A. NHMUK I.10732, (holotype like); B. NHMUK I.6737, C. NHMUK I.6653 (hooked white band); D. NHMUK I.6786 (heavily pigmented); E. VMNH 49735. From Kelly et al., 2017, fig. 6).

All of the specimens from the US were identified as *H. giebeli* (Huber et al., 2003), based on similarities with specimens figured in Whalley (1985) and Zeuner (1962). However, upon examination, 64 of them belong to *H. schlotheimi* and only three belong to *H. giebeli* based on the variation discussed herein. It has also been suggested that the elytral bands are veins (Zeuner, 1962) with Huber et al., (2003) suggesting that in North American specimens, veins are preserved black whereas Zeuner (1962) described British specimens as having white veins. There is no structural evidence to indicate that the bands of either colour are veins and given the variation in *H. schlotheimi* the bands are considered colouration.

Holcoptera giebeli (Handlirsch, 1907)

1845 ‘Harpalideous Carabidae’ Brodie, pp. 101, 124, pl. 10, fig. 2.

1907 *Holcoëlytrum giebeli* Handlirsch, p. 453, pl. 41, fig. 64.

1915 *Holcoptera giebeli* (Handlirsch); Cockerell, p. 480.

1962 *Holcoëlytrum giebeli* Handlirsch; Zeuner, p. 168, pl. 27, fig. 6–8.

1985 *Holcoptera giebeli* (Handlirsch); Whalley, p. 176, figs 83–87.

1999 *Holcoptera giebeli* (Handlirsch); Jarzembowski, p. 157, fig. 16B.

2010 *Holcoptera giebeli* (Handlirsch); Ross, p. 284, pl. 49, fig. 3.

Holotype.—NHMUK I.3581 (Fig. 3.51), Insect limestone (Penarth Group: Lilstock Formation); upper Rhaetian; Apperley, Gloucestershire.

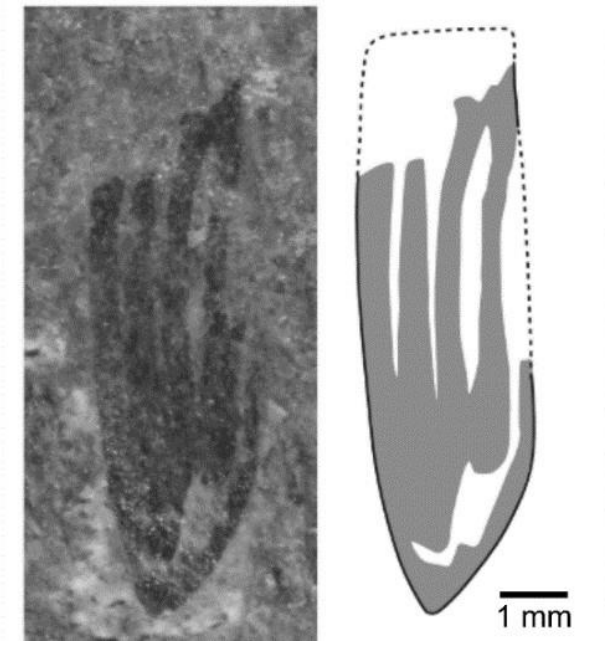

Figure 3.51. Holotype of *Holcoptera giebeli* (Handlirsch, 1907) (NHMUK I.3581), from Kelly et al. (2017, fig. 7), Appendix 4.

Additional material.—Rhaetian: NHMUK I.10977 Strensham. Hettangian: NHMUK I.6771 Binton. Hettangian–Sinemurian: YPM: 202526, 202506, 202550 Connecticut. Sinemurian: NHMUK: PI II 2171, PI II 2209 a,b, In.49209, In.59100, In.49621, In.49585, In.48163, In.49211, In.49619, In.53943, In.59393, PI II.3101 Black Ven; In.49244, In.59117, In.53981 (Whalley, 1985, fig. 86; Ross, 2010, pl. 49, fig. 3), In.53989 (Whalley, 1985, fig. 85; Jarzembowski, 1999, fig. 16B), In.49227, In.64009, In.53985, In.49611, In.64013, In.53937 (Whalley, 1985, figs 83 and 84), In.49229, In.49616 (Zeuner, 1962, pl. 27, fig. 6), In.51002 (Zeuner, 1962, pl. 27, figs 7 and 8), In.49204, In.64012, In.49570, In.59141, In.49563, In.53928 (Whalley, 1985, fig. 87), In.59153, In.49228, In.49239, In.59129, In.59145, In.53962, In.64010, In.53974, In.59148, In.64011, In.49610, In.49219, In.59138, In.59149, In.49618, NMW: 58.552.G1, 65.510.G164, 65.510.G533 a,b, 65.510.G538 a,b Stonebarrow;

65.510.G533 a,b Charmouth; 91.14G.10 a,b, 91.14G.11, 91.14G.12, 91.14G.14 a,b, 91.14G.15 a,b, 91.14G.16, 91.14G.17, 91.14G.18 a,b, 91.14G.19, 91.14G.20, 91.14G.21 a,b, 91.14G.22 a,b, 91.14G.24, 91.14G.27, 91.14G.28, 91.14G.32, 91.14G.38 a,b, 91.14G.39 a,b, 91.14G.44, 91.14G.46, 91.14G.47 a,b, 91.14G.9 Catherston Lane.

Emended diagnosis.—Elytral length 9.3–13.6 mm and width 2.7–4.2 mm; colour pattern is characteristic with five dark bands interspersed with light bands. Dark bands three and four fuse distally. Pronotum transverse, narrower than elytra with rounded lateral edges. Hind tarsi four segmented, first segment much longer than wide, second segment slightly longer than wide and apical segment wider than long with two hooks. Ventral and dorsal eyes. Tibial spur half the length of first tarsal segment.

Description.—Ventral aspect of NHMUK PI II.3101 (Fig. 3.52) preserved with elytra distorted so that dorsal elytra are also visible. Specimen is squashed, and certain segments have separated causing displacement of body parts and gaps in the overall structure. Total length of 15.5 mm and width of abdomen at widest point 7.5 mm. Elytral length 12 mm, width 4 mm. The elytral pattern is characteristic of *Holcoptera giebeli*. No hindwings are preserved. The abdomen has six visible sternites all of which appear to be have been covered completely by the elytra. The epipleura of the pronotum is preserved to each side of the prothorax of which the prosternum is visible. The legs are displaced and are not entirely clear but the pro– and mesocoxae can be seen in part and the metatibia and metacoxa in the counterpart. Also preserved in the part are a trochanter, several femora and tibiae with tibial spur and an almost complete metatarsus. Only one possible metacoxa is preserved in the counterpart but the part does show excavations where the metacoxae would have sat running through the first abdominal sternite laterally towards the elytral epipleura. Metafemur approximately 2 mm, metatibia approximately 2.5 mm expanding towards apex. At least four tarsal segments are present, the first three of almost equal size and the last one much smaller. The head appears prognathous but with no obvious mouthparts preserved, ventral pair of eyes preserved. There is a poorly preserved antenna which seems to show the most apical seven segments with a slight widening to a club in the most apical two segments.

Remarks.—Unfortunately, the holotype is very incomplete, however the preserved size and colour pattern is consistent with the abundant younger specimens from Dorset (see figures in Zeuner, 1962 and Whalley, 1985). The additional specimen from the Rhaetian is better preserved (Fig. 3.53A) and is clearly conspecific with specimens from after the TJB (Fig. 3.53B).

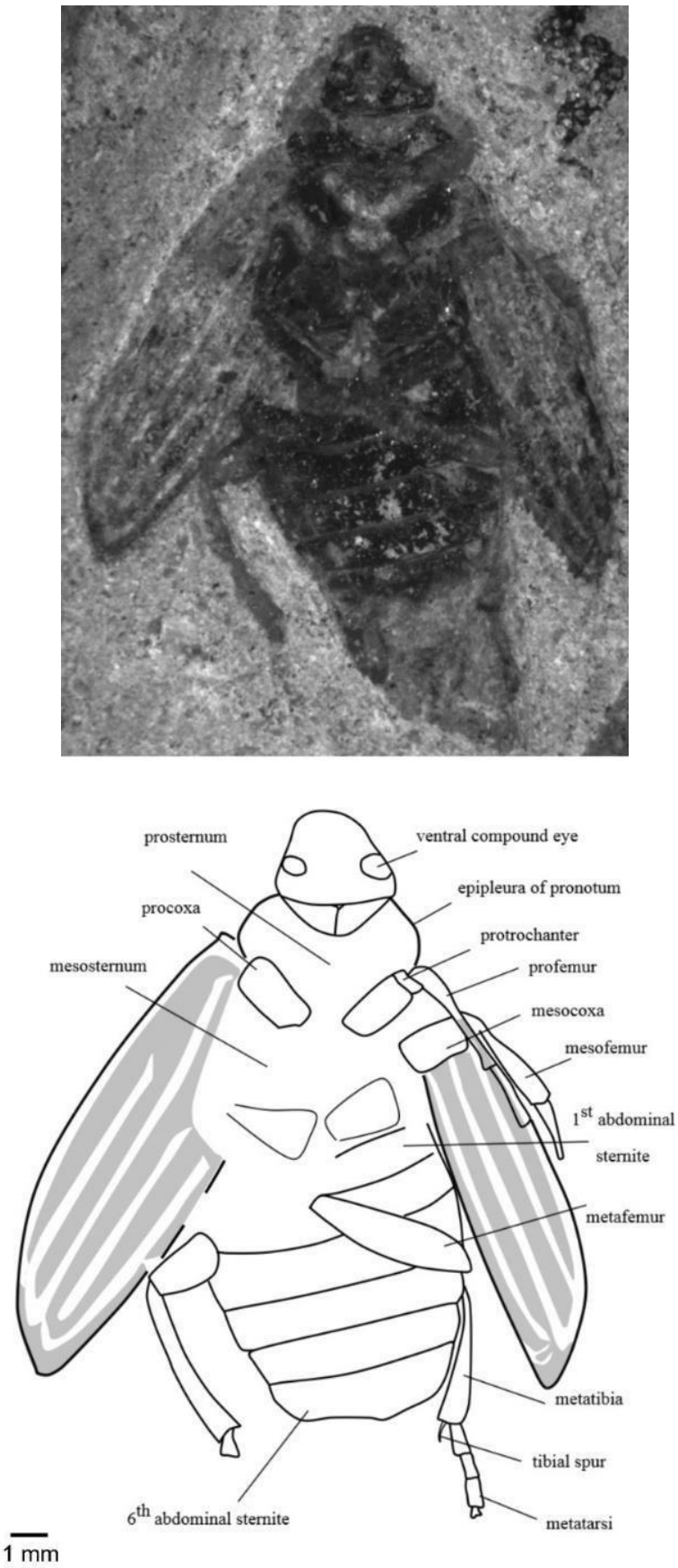

Figure 3.52. *Holcoptera giebeli* (NHMUK PI II 3101) from Kelly et al. (2017, fig. 8), Appendix 4.

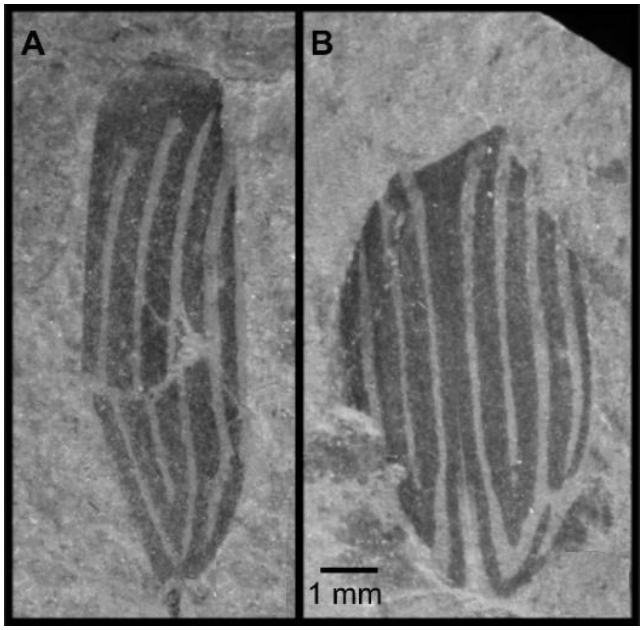

Figure 3.53. Examples of *H. giebeli* across the TJB, A. NHMUK I.10977 (Rhaetian), B. NHMUK I.6771 (Hettangian). From Kelly et al. (2017, fig. 10), Appendix 4.

Holcoptera pigmentatus Kelly et al., 2017

Holotype.—NHMUK I.10714 (Fig. 3.54). Penarth Group, Cotham or Langport member, upper Rhaetian, Brown's Wood, Warwickshire; Brodie Coll.

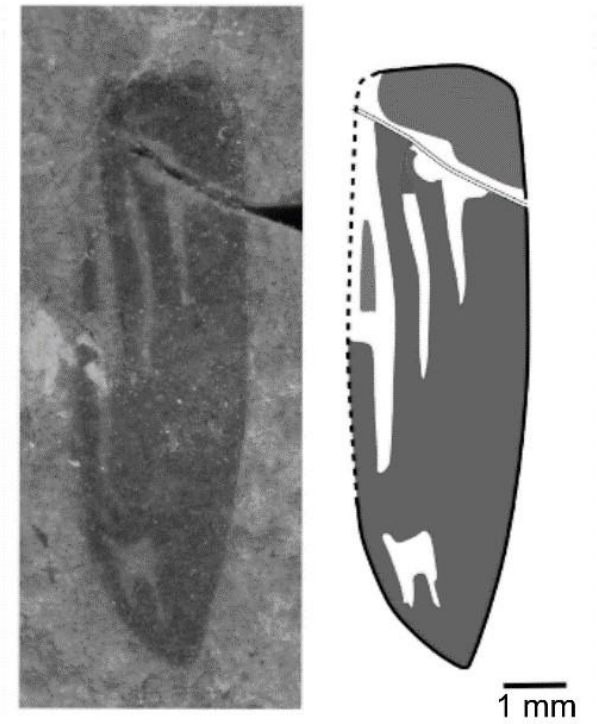

Figure 3.54. Holotype of *Holcoptera pigmentatus* Kelly et al., 2017 (NHMUK I.10714), from Kelly et al. (2017, fig. 11), Appendix 4.

Diagnosis.—Elytral length 9.3 mm, width 2.9 mm. Heavily pigmented, all dark bands fused, with three thin, slightly oblique pale bands getting progressively shorter towards the posterior margin. Pale spot at distal end.

Description.—The holotype is an isolated elytron. There is a crack basally and most of the anterior margin is not preserved making it appear as though a fourth white band exists, but this is a preservation artefact rather than a biological characteristic.

Remarks.—This specimen is intermediate in size between *H. schlotheimi* and *H. giebeli*. The colour pattern is similar to the heavily pigmented variety of *H. schlotheimi* though it has an extra pale band and pale spot, thus it constitutes a new species. The holotype of *H. giebeli* has broader dark bands than seen in most other specimens, and they slightly fuse though not to the same degree as seen in this specimen. Although there is only one known specimen, we consider the unique size and colour pattern as sufficient to warrant the description of a new species.

Holcoptera alisonae Kelly et al., 2017

1962 *'Holcoëlytrum schlotheimi'* Giebel; Zeuner, p. 170, pl. 27, fig. 5.
1985 *'Holcoptera schlotheimi'* Giebel; Whalley, p. 173, fig. 82.
1999 *'Holcoptera schlotheimi'* Giebel; Jarzembowski, p. 157, fig. 16A.
2010 *'Holcoptera schlotheimi'* Giebel; Ross, p. 284.

Holotype.—NHMUK In.59115 (Fig. 3.55). 'flatstones' (bed 83) of the Obtusum Zone: Obtusum Subzone (Lias Group: Charmouth Mudstone Formation: Black Ven Mudstone Member); Early Jurassic: Upper Sinemurian; Stonebarrow, Charmouth, Dorset. Jackson Coll.

Remarks.—This specimen was the neotype of *Holcoëlytrum schlotheimi* (Giebel, 1856) as assigned by Zeuner (1962), but it is distinct enough from *H. schlotheimi* to warrant description as a new species.

Paratypes.—NHMUK In.53958a, b, In.53990a, b (Whalley, 1985, fig. 82; Jarzembowski, 1999, fig. 16A), Stonebarrow (Upper Sinemurian); In.51019a, b from the 'flatstones' of Black Ven, II.2172a, b from the 'woodstones' of Black Ven, NMW 91.14G.137 from Catherston Road, all Upper Sinemurian.

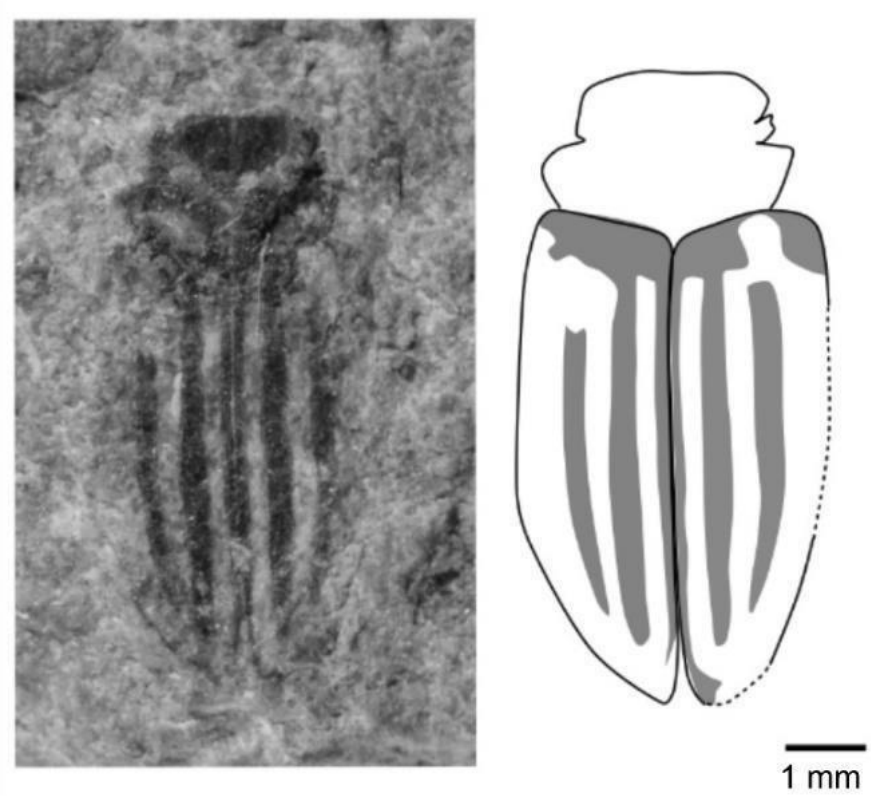

Figure 3.55. Holotype of *Holcoptera alisonae* Kelly et al., 2017 (NHMUK In.59115), from Kelly et al. (2017, fig. 12), Appendix 4.

Diagnosis.—Length 5.7–6.6 mm, Width 1.6–1.9 mm. Elytron with three dark longitudinal bands and three white bands. The dark bands do not merge distally; band one is floating; bands two and three connect to a dark patch at the base of the elytron. Band three is narrower and runs next to the elytral suture.

Description.—Holotype elytral length 6.5 mm and width 1.6 mm. Indication of pronotum and head are preserved but not well enough to make out any details.

Remarks.—This specimen was designated as the neotype of *H. schlotheimi* by Zeuner (1962). Although superficially similar to *H. schlotheimi*, on close examination this species only has three dark bands and they do not merge distally. These specimens are all from the Charmouth Mudstone Formation of Sinemurian age, and so younger than *H. schlotheimi* they also do not demonstrate the same high colour variation.

Conclusions.—The coleopteran genus *Holcoptera* was redescribed, *Holcoptera schlotheimi* (Giebel, 1856) and *Holcoptera confluens* Cockerell, 1915 were synonymised and the diagnosis of *Holcoptera*

giebeli (Handlirsch, 1907) was updated with details from a newly collected whole specimen found in Dorset which confirms its previously tentative placement in the Coptoclavidae. Two new species are described from elytra: *Holcoptera pigmentatus* Kelly et al., 2017 from the Rhaetian of Warwickshire and *Holcoptera alisonae* Kelly et al., 2017 from the Sinemurian of Dorset.

3.3.7 Neuroptera

This order contains the lacewings, mantidflies, and antlions which are characterised by rich wing venation with numerous crossveins and 'twigging' of veins towards the margin (Gullan and Cranston, 2010) (Fig. 3.56). They are related to the Coleoptera (Grimaldi and Engel, 2005), although superficially they do not appear so. The first reports of 'neuropterous insects' from the Mesozoic of Britain are found in Brodie (1845). *Actinophlebia* Handlirsch, 1906 was erected in the family Prohemerobiidae for species from the Toarcian of Germany and included several of Brodie's specimens (Handlirsch, 1906). ? *Actinophlebia intermixta* (Scudder, 1885) was originally incorrectly described as a cockroach, *Pteroblattina intermixta* (Scudder, 1885; figured in Scudder, 1886, pl. 48, fig. 9). *Prohemerobius* Handlirsch, 1906 was also erected for several species from the Toarcian of Germany. *Paractinophlebia* Handlirsch, 1906 was also erected for *Paractinophlebia curtisi* (Scudder, 1886) which is also originally incorrectly described as a cockroach, *Pteroblattina curtissi* (Scudder, 1885, pl. 48, fig. 16). This genus was transferred to Prohemerobiidae by Whalley (1988).

Tillyard (1933) described *Actinophlebia anglicana* Tillyard, 1933 (fig. 2) and erected *Megapolystoechus* Tillyard, 1933 for the new species *M. magnificus* Tillyard, 1933 (fig. 1) and placed it in the family Prohemerobiidae. Martynova (1962) moved the genus to Mesopolystoechotidae but Carpenter (1992) considered the genus too poorly known to assign to a family. Whalley (1988) described *Prohemerobius aldertonensis* Whalley, 1988 (figs 11 & 13), the first English representative of the genus and *Archeosmylus complexus* Whalley, 1988 (figs 1 & 3) and *A. alysius* Whalley, 1988 (figs 2 & 4) a genus previously only known from Australia (Riek, 1953; 1955).

Actinophlebia was considered in Brongniartiellidae in the superfamily Psychopsidoidea by Martynova (1949; 1962) and Carpenter (1992). Ponomarenko (1995) considered *Actinophlebia* to belong to Osmylopsychopsidae and most species to *Parhemerobius*. Ansorge (1996) did not cite Ponomarenko (1995) and followed Carpenter (1992), considering *Actinophlebia* in Brongniartiellidae. andersen (2001) transferred *Actinophlebia* to Prohemerobiidae, based mainly on the absence of the *vena triplica*, but also due to the 'narrower Sc space compared to R1 space'. andersen did not cite Ponomarenko (1995) but rather followed Martynova, Carpenter, and Ansorge. (Makarkin and Archibald, 2005) consider *Actinophlebia* in Osmylopsychopidae but did not cite (andersen, 2001). (Jepson et al., 2012) reported *Actinophlebia* in Brongniartiellidae for some authors and

Osmylopsychopidae for others. The authors did not cite andersen (2001) but considered that the genus was more likely closer to Prohemerobiidae.

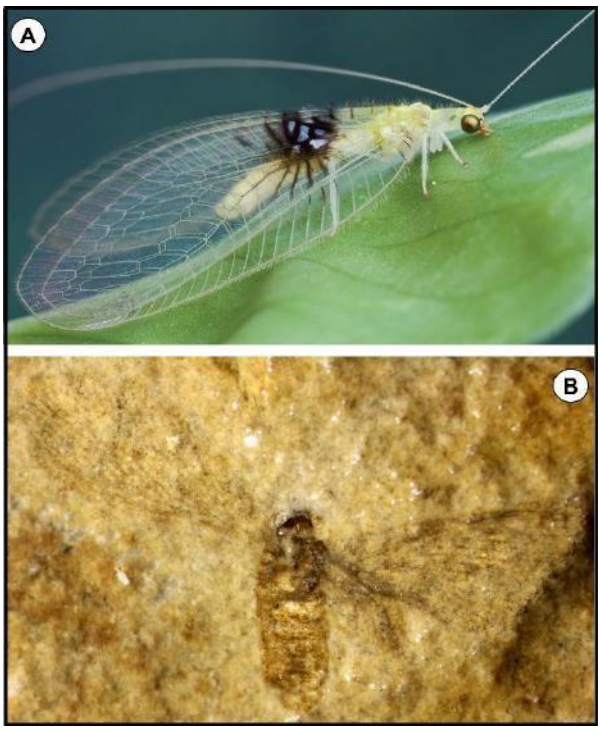

Figure 3.56. Examples of lacewings of the order Neuroptera. A. Extant lacewing, Semachrysa jade (photo by Hock Ping Guek), B. Jurassic lacewing, *Archaeosmylus alysius* (NHMUK I.3318).

Systematic Palaeontology

Order NEUROPTERA Linnaeus, 1758

Family PROHEMEROBIIDAE Handlirsch, 1906

Genus ACTINOPHLEBIA Handlirsch, 1906

Type species.—Pterinoblattina megapolitana Geinitz, 1856.

Diagnosis.—As in Whalley, 1988: subtriangular forewing with numerous C veinlets; Sc, R, and Rs close together but running separately to apex; Rs with 12–16 branches.

"Neur:Proh. sp. nov. 1"

Holotype.—OUMNH J.47007 (Fig. 3.57), Planorbis Zone (Lias Group: Blue Lias Formation: Wilmcote Limestone Member); Early Jurassic: Lower Hettangian; Binton, Warwickshire.

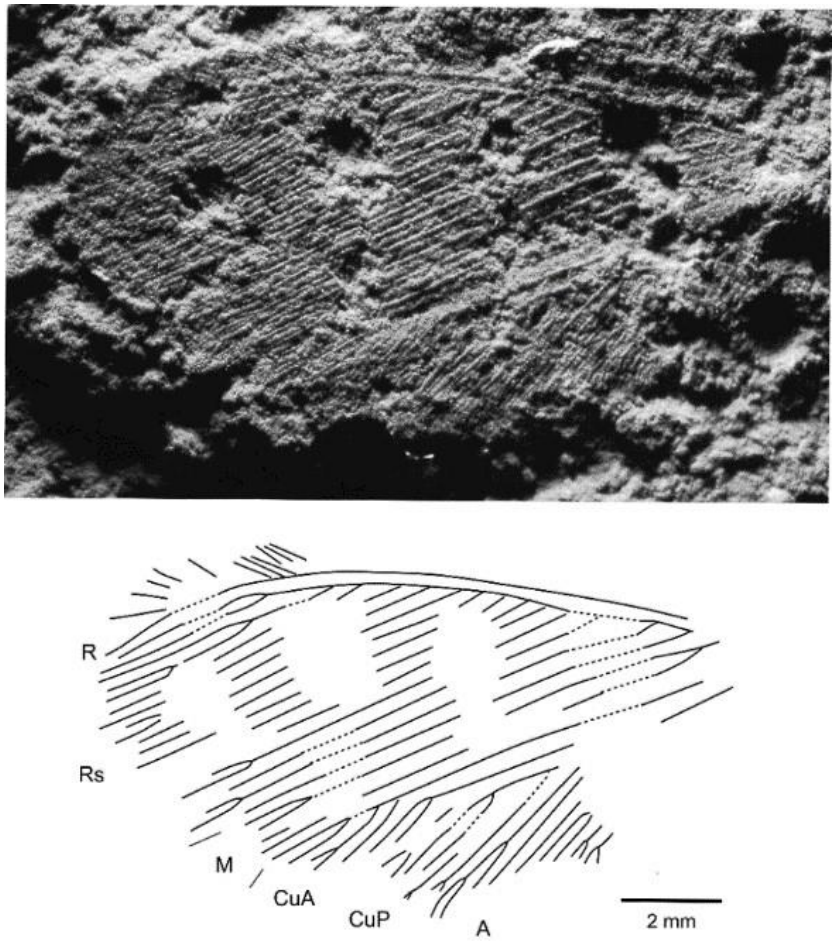

Figure 3.57. Holotype of "Neur:Proh. sp. nov. 1" (OUMNH J.47007), for Kelly et al. (In preparation a).

Diagnosis.—Forewing characters known, preserved length 12.1 mm. Older *Actinophlebia* (20 my older than *A. intermixta*); stalks of CuA and CuP less curved; slightly larger (total length of *A. intermixta* estimated as 12 mm by Scudder, 1885, whereas this species is probably 15–16 mm based on preserved length of 12.1 mm).

Description.—Similar shape and venation to other species of *Actinophlebia*; costal region faint but most main veins persevered at least partially. Banded appearance is due to poor membrane preservation as there are no veins preserved in these lighter areas either.

Genus PROHEMEROBIUS Handlirsch, 1906

"Neur:Proh. sp. nov. 2"

Holotype.—NHMUK In.64664 (Fig. 3.58) Jarzembowski coll., Insect limestone, Cotham Member (Penarth Group: Lilstock Formation); Late Triassic: upper Rhaetian; Wainlode Cliff, Gloucestershire.

Additional material.—RS/NEUR 1 from Blue Anchor, held in the private collection of Rob Coram.
Diagnosis.—Fragmentary forewing characters known, preserved length 8.3 mm. Combination of the following characters: six branches of Rs; MA bifurcated with posterior branch simple; MP bifurcated twice; CuA and CuP pectinately branched. Spots between MA and MP. Costal area relatively broad.

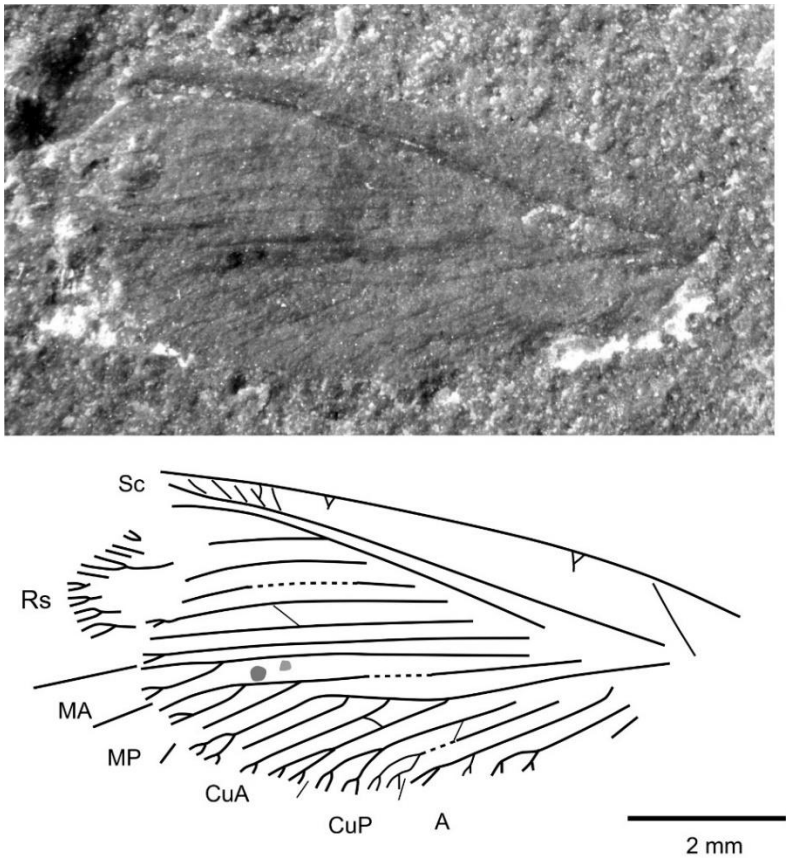

Figure 3.58. Holotype of "Neur:Proh. sp. nov. 2" (NHMUK In.64664), for Kelly et al. (In preparation a).

Remarks.—This species is similar to *P. septemvirgatus* Bode, 1953 but costal region much broader and Sc does not appear to extend as far towards the apex although it is not well preserved; *P. mediolatus* Bode, 1953 except MA is not simple, CuA does not have five branches and the costal margin is broader; *P. quatuoripictus* Bode, 1953 except CuP is not similar; *P. sexfasciatus* Bode, 1953 and *P. prodromus* Handlirsch, 1906 except posterior branch of MA is simple. The species *sexfasciatus* was identified as a junior synonym of *prodromus* by Ansorge (1996), in the genus *Sibithone* later replaced to *Prohemerobius* (Makarkin, 1999), however subsequent authors list *P. sexfasciatus* as a separate species (Makarkin and Menon, 2007; Khramov, 2011). Based on the figures of *P. prodromus* (Ansorge, 1996, fig. 49) and *P. sexfasciatus* (Ponomarenko, 1995, figs 15–19), Sc and R curve and terminate in the same fashion; there are similar numbers of veins in the radial, median and cubital

sectors and they bifurcate in a similar manner but MP in *P. prodromus* appears to be directly attached to Rs whereas in *P. sexfasciatus* it appears to be free to the base; also the apical forks of MP appear to be deeper in *P. sexfasciatus*; CuA is more developed in *P. prodromus* with several more bifurcations than seen in *P. sexfasciatus.* Further examination of the holotypes would be necessary to determine whether these are conspecific or not.

Conclusions.—Two new lacewing species were described, one in Prohemerobiidae from the Hope collection, "Neur:Proh. sp. nov. 1" and one in Prohemerobius from the Jarzembowski collection, "Neur:Proh. sp. nov. 2."

3.3.8 Raphidioptera

Two species of snakefly were described by Whalley (1985) from the Dorset Coast, Mesoraphidiidae: *Mesoraphidia confusa* (Whalley, 1985) (Fig. 3.59) and Baissopteriidae: *Priscaenigma obtusa* Whalley, 1985 (Fig. 3.60), which did not require revision. The former was originally described in the genus *Metaraphidia* by Whalley (1985) but was later transferred to *Mesoraphidia* by Whalley (1988), although it is usually still considered in the former (Jepson and Jarzembowski, 2008). The species belongs to *Metaraphidia* based on the similarity of characters with *Metaraphidia vahldieki* Willmann, 1994 such as, multiple crossveins in pt area (although this is seen in *Mesoraphidia*, e.g. *M. elongata* Martynov, 1925, cua-cup crossveins are present), lack of crossveins between CuA and CuP (Jepson and Jarzembowski, 2008; Jepson et al., 2009).

The ordinal taxonomy of *Priscaenigma* has been called into question. (Ponomarenko, 2002b) considered that it did not belong to Raphidioptera based on the following characters: SC meeting R rather than C, R close to the anterior margin almost to the apex, and the absence of the characteristics anal cell. Whereas, (Engel, 2002) considered that it did belong to the Raphidioptera and erected a new family within this order for the genus, Priscaenigmatidae, following the conclusion of Willmann (1994) that the genus did not belong to Baissopteriidae. (Aspöck and Aspöck, 2004) agreed with Ponomarenko and dismissed *Priscaenigma* from the Raphidioptera based on the extension of Sc to the apex and not the anterior margin as in other raphidiopterans. (Bechly and Wolf-Schwenninger, 2011) reject attempts to remove the genus from Raphidioptera based on the results of a phylogenetic analysis and retain the suborder Priscaenigmatomorpha. They regard previous evidence as insufficient stating that the length of Sc is a 'desirable definition' for the order but that the evidence does not necessarily support it. (Liu et al., 2014) retain Priscaenigmatomorpha in the Raphidioptera but reject most of Bechly and Wolf-Schwenninger's proposed synapomorphies stating that a rigorous phylogenetic analysis is necessary.

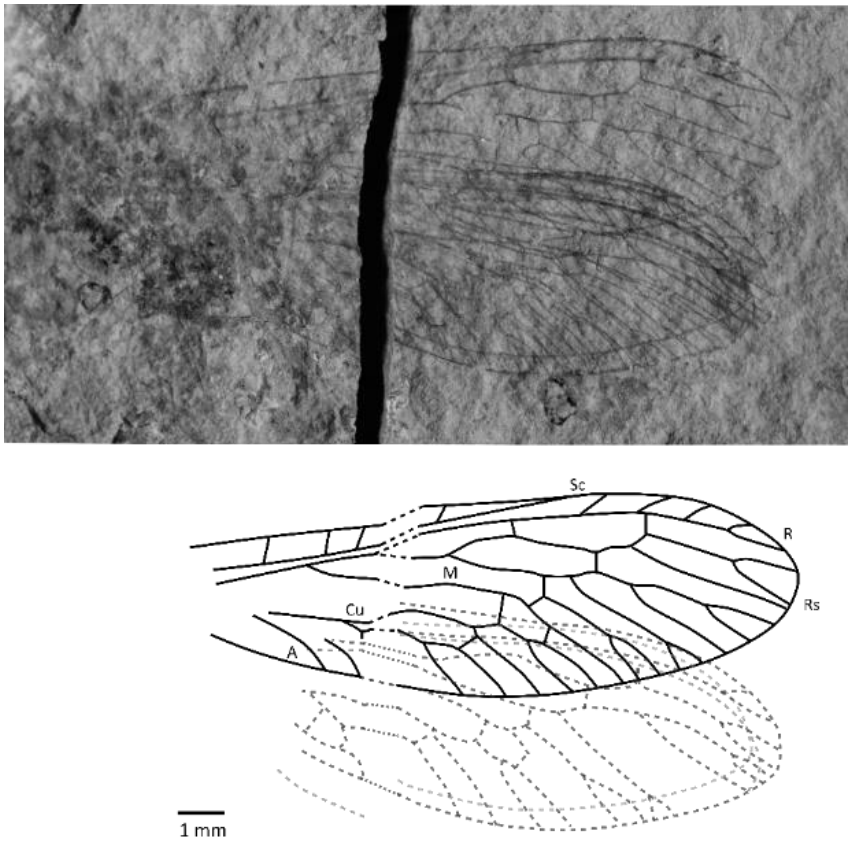

Figure 3.59. Holotype of *Metaraphidia confusa* Whalley, 1985 (GSM 117552).

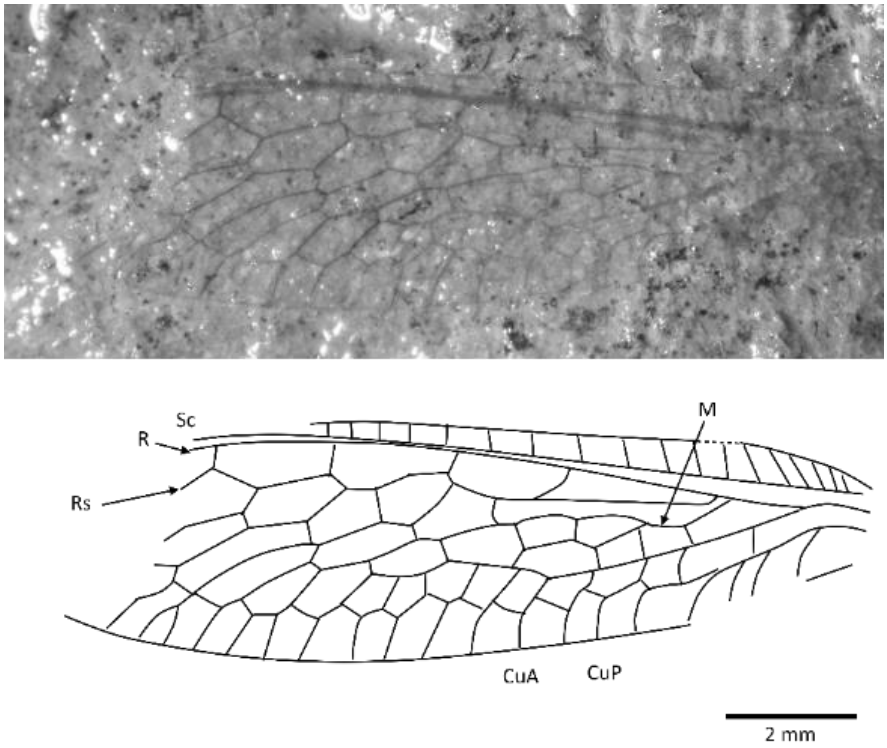

Figure 3.60. Holotype of *Priscaenigma obtusa* Whalley, 1985 (NHMUK In.53898).

3.3.9 Trichoptera

This order contains the caddisflies, adults have a similar morphology to moths, highlighting their close relationship with the Lepidoptera (Fig. 3.61). Whereas Lepidoptera ('scale-winged') have a layer of scales on their wings, however, Trichoptera ('hairy-winged') usually have a layer of hairs, but there are exceptions and some caddisflies are known to have scales (Huxley and Barnard, 1988). Most larvae are aquatic although some can be semi-aquatic or terrestrial and they are among the few insects to have radiated into the marine realm (Riek, 1977). Caddisfly wing fossils can be difficult to distinguish from early Lepidoptera and stem-Amphiesmenoptera. Trichoptera and Lepidoptera evolved from stem-Amphiesmenoptera early in the Mesozoic (Grimaldi and Engel, 2005) with the extinct family Necrotauliidae filling an undefined space within or between the stem-Amphiesmenoptera and the evolving Lepidoptera and Trichoptera.

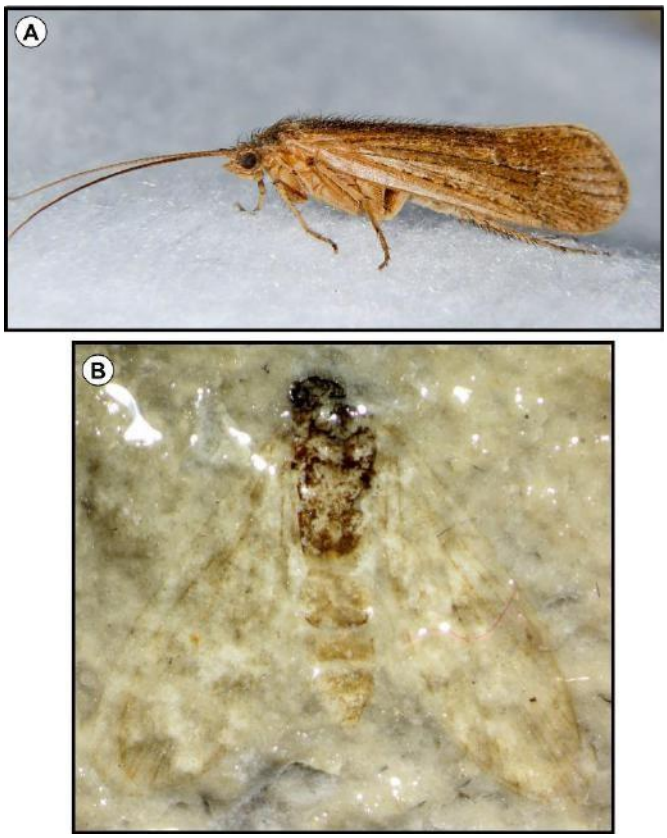

Figure 3.61 Examples of caddisflies of the order Trichoptera. A. Extant caddisfly, *Limnephilus frijole* (photo by B. Newell), B. Jurassic caddisfly, *Necrotaulius* sp. (NHMUK I.11259).

The family Necrotauliidae was erected by Handlirsch (1906), for the new genus *Necrotaulius* which included *N. furcatus* (Giebel, 1856) and *N. liasina* (Giebel, 1856) from Britain, originally named in the mecopteran (scorpionfly) genus *Orthophlebia*. Also, the genus *Mesotrichopteridium* Handlirsch, 1906 was erected for the new species *M. pusillum* Handlirsch, 1906. *N. liasina* and *N. furcatus* were synonymised by Tillyard (1933), giving the latter priority. Tillyard also described *N. westwoodi*

Tillyard, 1933, *N. stigmaticus* Tillyard, 1933, *N. apicalis* Tillyard, 1933 and *N. pygmaeus* Tillyard, 1933 from British material. *N. parvulus* (Geinitz, 1884) was transferred from the genus *Orthophlebia* and *N. pygmaeus* was made a junior synonym by Ansorge (1996). *Necrotaulius* is the only known genus of Trichoptera known from the English Triassic/Jurassic.

Systematic Palaeontology

Superorder AMPHIESMENOPTERA Kiriakoff, 1948

Order TRICHOPTERA Kirby, 1813

Family NECROTAULIIDAE Handlirsch, 1907

Emended Diagnosis.—Forewings with the following combination of characters: R simple; Rs with two forks (each with two branches); M with two forks (each with two branches); CuA forked; m-cu cross vein (or base of CuA) present; 2A and 3A merge, and then merge with 1A which terminates on the posterior margin. In hindwing, MP simple and anal veins are simple, terminating on the posterior margin. Hairs present on forewing and around wing margins of both fore- and hindwings (if preserved).

Genus NECROTAULIUS Handlirsch, 1907

Type species.—Necrotaulius parvulus (Geinitz, 1884)

Emended Diagnosis.—Sc simple, r-m crossvein absent, CuA connected by 'Y-shape' to M and CuP; labial palps longer, second segment more elongate than first or third.

Necrotaulius parvulus (Geinitz, 1884)

Holotype.—EMAUG 119/7 (Ansorge, 2002) from the Falciferum Zone of the Posidonia Shale Formation (Lower Toarcian), Schwinz near Dobbertin, Germany.

Additional material.—See Ansorge, 2002 for list of Lower Toarcian German specimens. British Toarcian: NHMUK I.15014 (holotype of *Necrotaulius pygmaeus* Tillyard, Fig. 3.62) and I.11425, both Dumbleton and TTNCM 39/2011/0733, Ilminster, Somerset.

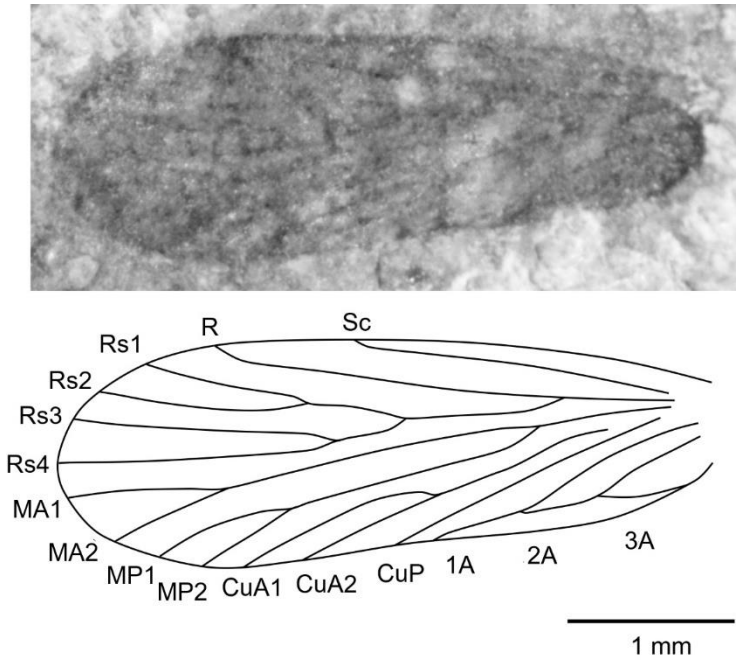

Figure 3.62. Example of English *Necrotaulius parvulus* (Geinitz, 1884), holotype of *N. pygmaeus* (NHMUK I.15014), from Kelly et al. (2018a, fig. 3), Appendix 5.

Diagnosis.—After Ansorge (2002) forewing length 2.4–3.6 mm and hindwing length approximately 85% of forewing. sc-r crossvein; no pterostigma.

Genus AUSTAULIUS Kelly et al., 2018b

urn:lsid:zoobank.org:act:D1FBC755-D8BD-45DA-9934-9C78F029DF8E

Type species.—*Austaulius furcatus* (Giebel, 1856).

Diagnosis.—Sc with one anterior branch, r-m crossvein absent, CuA fuses with M for a short distance near the base then with an oblique cross-vein connecting MP+CuA to CuP; labial palps shorter; second segment about same length as first segment.

Remarks.—Clearly the form of CuA was misinterpreted by Tillyard (1933) and begs the question as to whether any other *Necrotaulius* species have been misinterpreted. Other *Necrotaulius* holotypes were checked in person by the senior author. The following do not possess the diagnostic form of CuA as seen in *Austaulius*: *N. parvulus* (Geinitz, 1884) (EMAUG 119/7) from the Upper Lias of Germany; *N. kubekovi* Sukacheva, 1985 (PIN 1255/193) from the Middle Jurassic of Russia; *N. minutissimus* Sukacheva, 1990 (PIN 3063/742), *N. minutus* (Sukacheva, 1968) (PIN 2066/1303) and *N. tener* Sukatsheva, 1990 (PIN 3015/819) (Grimaldi and Engel, 2005, fig. 13.1 and Rasnitsyn and Quicke,

2002, fig. 283) from the Late Jurassic of Russia and Kazakhstan and *N. kritus* Lin, 1986 (NIGPAS 70078) from the Middle Jurassic of China. *N. fascialatus* Hong, 1983 and *N. qingshilaense* Hong, 1984 were described from the Late Jurassic and Early Cretaceous of China respectively. Unfortunately, it is not known where Hong's holotypes are although researchers at NIGPAS have been searching for them (Wang Bo, pers. comm., 2016). Based on Hong's figures it appears that the basal area of the wing is not preserved in *N. fascialatus* (Hong, 1984, fig. 46), the character may be present in *N. qingshilaense* (Hong, 1984, fig. 47) but it is not at all clear, the holotype would need to be examined. *N. mantellorum* Jarzembowski, 1991 (Booth Museum, Brighton 014897/8) was described from the Early Cretaceous of England. It requires re-examination to confirm if it belongs to *Necrotaulius* or not.

Austaulius furcatus (Giebel, 1856)

1845 'Neuropterous insects' Westwood in Brodie, p. 127, pl. 9, figs 16, 17.
1856 *Orthophlebia furcata* Giebel, p. 261.
1856 *Orthophlebia liasina* Giebel, p. 261.
1878 *Orthophlebia furcata* Giebel; Goss, p. 145.
1878 *Orthophlebia liasina* Giebel; Goss, p. 145.
1891 *Orthophlebia furcata* Giebel; Scudder, p. 156.
1891 *Orthophlebia liasina* Giebel; Scudder, p. 157.
1893 *Orthophlebia furcata* Giebel; Woodward, p. 367.
1893 *Orthophlebia liasina* Giebel; Woodward, p. 367.
1907 *Necrotaulius furcatus* (Giebel); Handlirsch, p. 484, pl .42, fig. 37.
1907 *Necrotaulius liasinus* (Giebel); Handlirsch, p. 485, pl. 42, fig. 38.
1933 *Necrotaulius furcatus* (Giebel); Tillyard, p. 62, figs 23–25.
1933 *Necrotaulius stigmaticus* Tillyard, p. 65, fig. 27.
1933 *Necrotaulius westwoodi* Tillyard, p. 65, fig. 26.
1933 *Necrotaulius apicalis* Tillyard, p. 66, fig. 28.
1978 *Necrotaulius furcatus* (Giebel); Willmann, p. 115.
1992 *Necrotaulius westwoodi* Tillyard; Carpenter, p. 362, fig. 201, 7.
1999 *Necrotaulius furcatus* (Giebel); Jarzembowski, p. 159, text-fig. 18A, B.
2010 *Necrotaulius furcatus* (Giebel); Jarzembowski and Palmer, p. 170, fig. 4.19.

Holotype.—YORYM YM 815/ NHMUK I.11522 (Fig. 3.63) from the Cotham Member of the Penarth Group (Rhaetian), Aust, Gloucestershire.

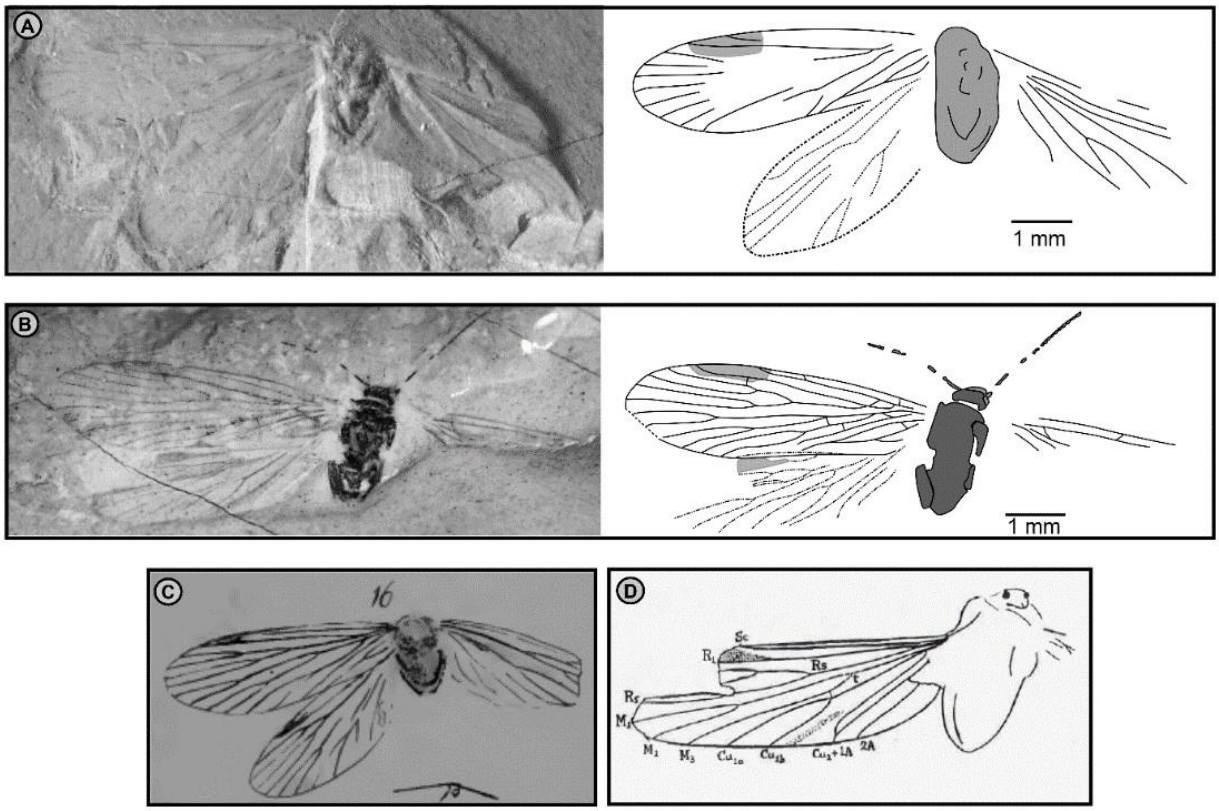

Figure 3.63. Holotype of *Austaulius furcatus* (Giebel, 1856), A. YORYM YM 815; B. NHMUK I.11522; C. original holotype figure (Brodie, 1845, pl. 9, fig. 16); D. Figure of 'holotype' (Tillyard, 1933, fig. 25). From Kelly et al. (2018a, fig. 4), Appendix 5.

Remarks.—The holotype of this species was originally reported as YM 815 (Pyrah, 1976) with the counterpart being sent to the 'British Museum' (NHMUK) (note by R. Wootton in specimen box at YORYM). NHMUK I.11522 was later reported as the holotype by Tillyard (1933) who considered that the differences in the specimens was due to breakage after the original holotype figure. Based on the original figure of the holotype by Brodie (1845, pl. 9, fig. 16) and writing on the rock of the specimens, however, it is clear that the first report was correct. YM 815 matches the holotype figure by Brodie (1845, pl. 9, fig. 16) and written on the rock in Brodie's handwriting is "Pl 9 F 16". Figure 3.63 shows the specimens involved and copies of the figures from Brodie (1845) and Tillyard (1933). It is unclear why Tillyard figured I.11522 without the very prominent left forewing; he did suggest that the specimen had broken since Brodie's original figure, so perhaps it was further prepared after Tillyard had figured it, revealing the forewing. Although the part and counterpart look different, there is a calcite vein that cuts diagonally across the hindwing at the same position in both parts.

Additional material.—Rhaetian: NHMUK I.11545, I.11544 (previous holotype of *O. liasina*, Brodie (1845, pl. 9, fig. 17), I.11534; YORYM: YM1984/7F, YM1984/6F, YM1984/1F from Aust Cliff; I.3081 from Wainlode Cliff (previous holotype of *N. apicalis*, fig. 3.64a); one other in the Coram collection collected from Blue Anchor. Hettangian: I.11019 from Copt Heath; I.11584 from unknown

locality in England ("W" on museum label) (previous holotype of *N. stigmaticus* fig. 3.64b); I.11761 (previous holotype of *N. westwoodi* fig. 3.64c) and 11574 both from unknown localities in England.

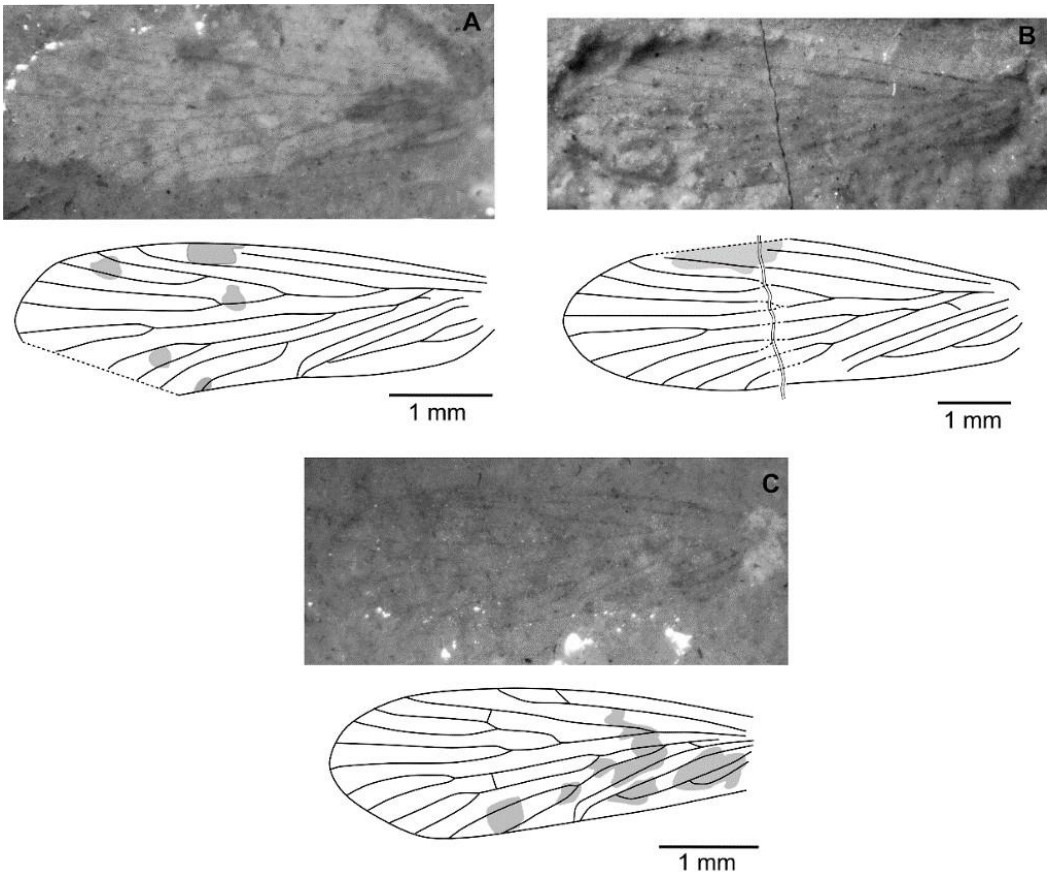

Figure 3.64. Previous holotypes now considered conspecific with *Austaulius furcatus* (Giebel, 1856), A. '*Necrotaulius apicalis*' Tillyard, 1933 (NHMUK I.3081); B. '*N. stigmaticus*' Tillyard, 1933 (NHMUK I.11584); C. '*N. westwoodi*' Tillyard, 1933 (NHMUK I.11761). From Kelly et al. (2018a, fig. 5), Appendix 5.

Diagnosis.—Forewings 4.3–5.6 mm in length, 1.4–1.8 mm in width. Anterior fork (F1) of Rs branching point is almost in line with the branching point of posterior fork (F2), or slightly distal.

Description.—Holotype forewing 5.3 mm in length. It is an almost whole specimen with both forewings wholly preserved (one on each part); right hindwing nearly complete. Body, head and antennae also preserved in the counterpart but poorly. One antenna with 15 antennomeres preserved including scape. In forewing Sc terminating on C just beyond mid-wing, with two cross-veins between Sc and C; R simple, reaching anterior margin in apical quarter of the wing within the pterostigma; oblique cross-vein near base between R and Sc; Rs splits from R in basal quarter further bifurcating into two forks of subequal length (posterior fork slightly longer than anterior). M lying very close to R at base and fused with CuA shortly after leaving CuP for a short distance; M bifurcates forming two forks, the anterior shorter than the posterior; one cross-vein between M and CuA; CuP is preserved

almost to the posterior margin; one cross-vein between CuA and CuP. Additional cross-vein between 1A and 2A near the base. Hindwings are poorly preserved but, in the counterpart, it seems that the venation is similar except there are three veins in the medial system rather than four, the posterior vein being simple. Colour pattern evident in most specimens although may be faint.

Austaulius haustrum Kelly et al., 2018a
urn:lsid:zoobank.org:act:09920586-B224-437C-A567-46808E8D1AAE

Holotype.—NHMUK II 3103 a and b (Fig. 3.65), Sinemurian, Turneri Zone, Brooki Bed, Monmouth Beach, Lyme Regis, Dorset, UK. Coram collection.

Diagnosis.—Forewing length 4.7 mm, width 1.8 mm. Anterior fork (F1) of Rs branches distally of branching point of posterior fork (F2), much further than in *A. furcatus.*

Description.—The holotype is a well-preserved specimen with two forewings and a partial hind wing, thorax, head, some antennomeres, some leg segments, maxillary and labial palps and the haustellum. Pronotum is small and heavily sclerotised. Fore coxa broader than the fore femur, mid coxa appears broader but not well preserved. Head is hypognathous. Maxillary palps are longer than the labial palps, two elongate segments of one palp preserved; three labial palp segments preserved (as well as another unidentified palp with two segments), attached to the haustellum. Eye socket appears large, but only a small portion of the actual eye is preserved and there is a groove above the eye where the lateral ocellus would be found. The apex of CuP appears to be desclerotised as in *A. furcatus*.

Remarks.—This specimen was figured by Coram (2014, fig. 5) as a ‘caddisfly-like necrotauliid’. This is the only necrotauliid specimen to preserve the haustellum. As discussed in the introduction, this is the only specified adult synapomorphy for Trichoptera (Holzenthal et al., 2007) and suggests that the Necrotauliidae are trichopterans.

Conclusions.—Necrotauliidae was confirmed in Trichoptera by description of a new genus, *Austaulius* Kelly et al., 2018a, which preserves synapomorphic traits of the Trichoptera not previously described. All previous species known from the Lilstock Formation/Blue Lias Formation of England were transferred to *Austaulius*: *Necrotaulius apicalis* Tillyard, 1933; *N. westwoodi* Tillyard, 1933; and *N.* (Giebel, 1856), were synonymised, with the latter being the senior synonym. Only one species of *Necrotaulius* is represented in England, *N. parvulus*, which was refigured.

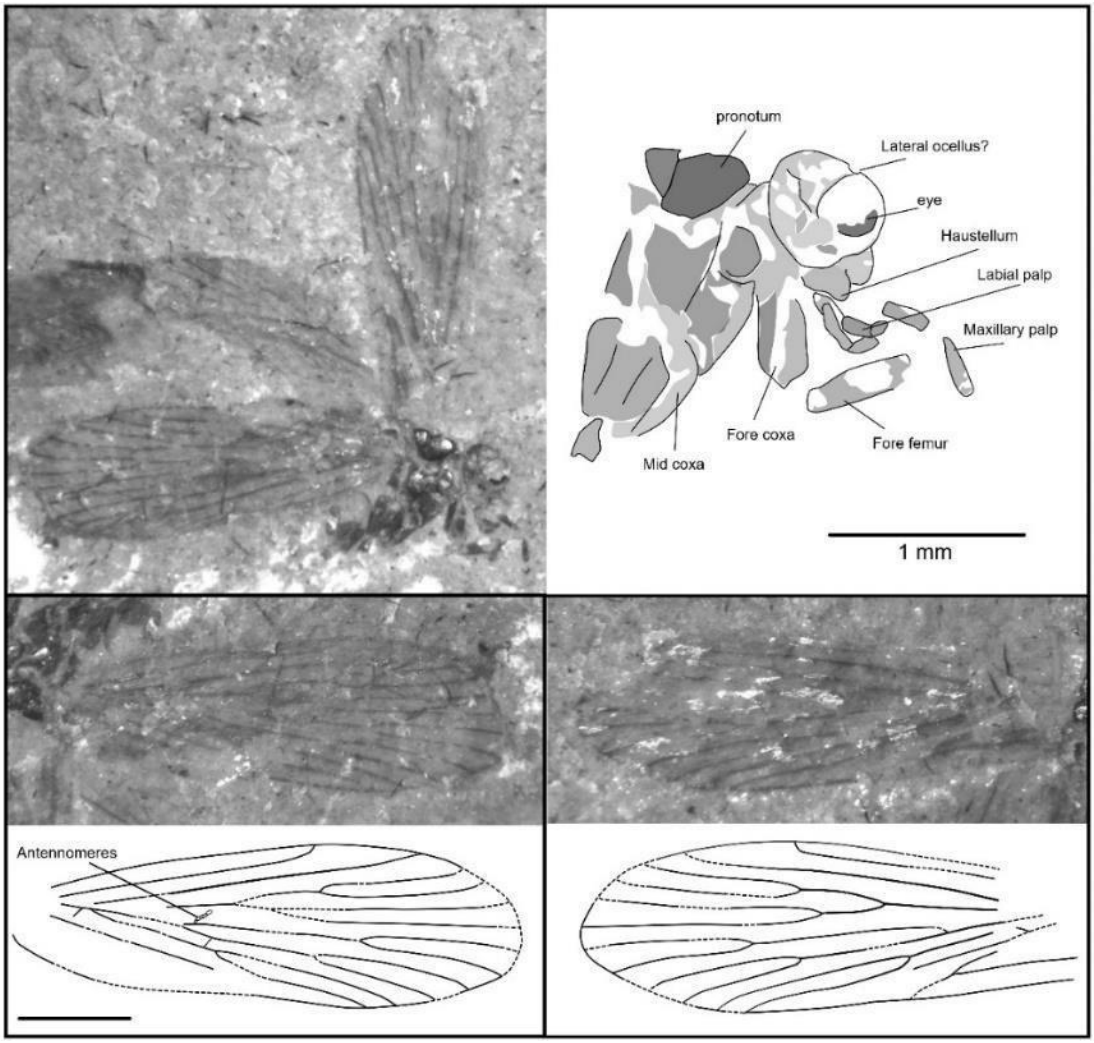

Figure 3.65. Holotype of *Austaulius haustrum* Kelly et al., 2018b (NHMUK II 3103 a and b, bottom left figure is the right forewing of the holotype flipped so the costal margin is on top. From Kelly et al. (2018a, fig. 6), Appendix 5.

3.3.10 Lepidoptera

One species of Lepidoptera is known from the Dorset Coast and did not require any further revision. It was described by Whalley (1985) as *Archaeolepis mane* (Fig. 3.66) in a newly erected family, Archaeolepidae (=Archaeolepiidae in Sohn et al. 2012). It was suggested to possibly belong to Eolepidopterigidae (Skalski, 1990) ("?Eolepidopterigidae") but is still considered to be in Archaeolepidae (Sohn, 2012; Mey et al., 2017; van Eldijk et al., 2018; Zhang et al., 2018). It was previously considered to be the oldest known fossil which could be confidently assigned to the Lepidoptera (Kristensen and Skalski, 1998) until fossil lepidopteran scales were uncovered from the Triassic of Germany (van Eldijk et al., 2018).

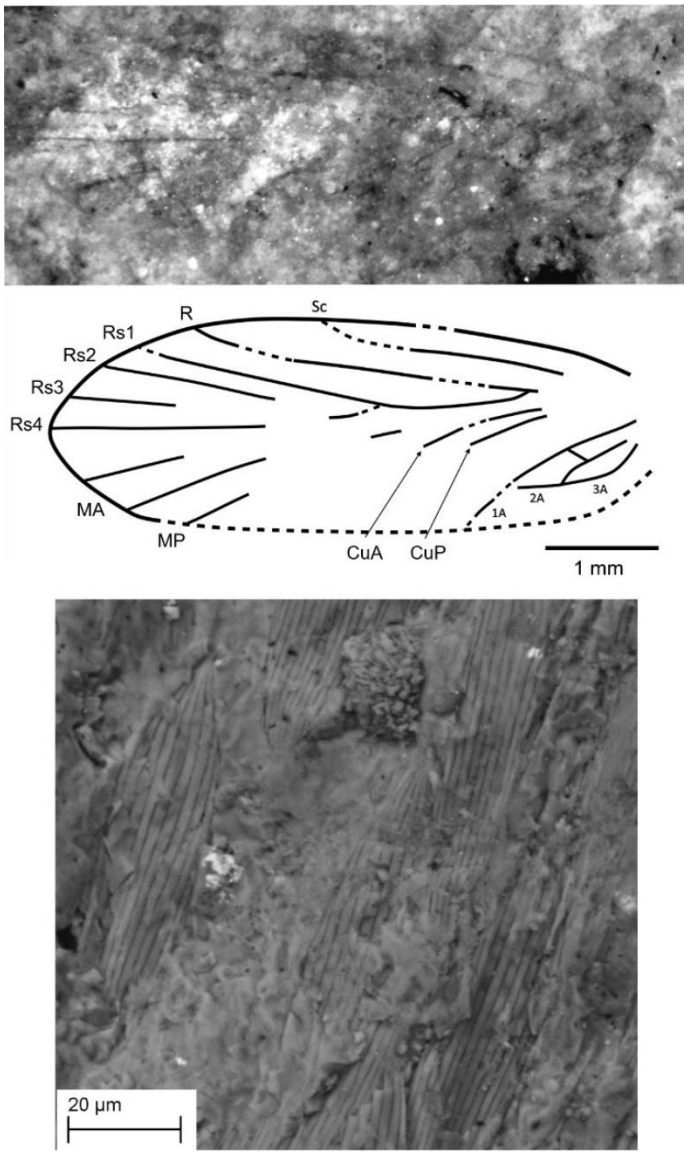

Figure 3.66. Holotype of *Archaeolepis mane* (NHMUK In.59397), including SEM micrograph of scales. Modified from Zhang et al. (2018, fig. S1), the figure was put together by RSK for that study.

3.4 Overall Conclusions

Several key groups of insects were revised during the course of the project. Given the high diversity of insects, it was not possible to revise all of the insects present in the collections, so we concentrated on those with the highest impact on faunal composition compared to the effort required to revise, i.e. the more abundant or speciose taxa or those for which the taxonomy was easily fixed by refiguring some specimens. These were: Odonata: Campterophlebiidae and Liassophlebiidae; Dermaptera; Orthoptera: Bintoniellidae, Elcanidae, Haglidae, and Locustopseidae; Hemiptera: Cicadomorpha and Fulgoromorpha; Coleoptera: Coptoclavidae; Neuroptera; and Trichoptera. We have described 13 new species, six new genera and one tentative new family from the Late Triassic/Early Jurassic of England. We have also synonymised or recombined a further 10 species/genera, emended the diagnosis for 12 species/genera, and removed four species as *nomen dubia*.

Chapter 4. Taxic diversity and palaeoecology of British Late Triassic/Early Jurassic insect assemblages

4.1 Introduction

The Late Triassic and Early Jurassic deposits of England represent a promising resource for investigating insect diversity dynamics through the TJB. It is the only place in the world to preserve large numbers of insects from formations which can be precisely aged to the upper Rhaetian and Lower Hettangian. It is also one of the most prolific areas for Sinemurian aged insects that can be precisely aged to individual horizons. Although the insect-bearing beds are not preserved in a single section, they are generally preserved in similar facies—white/grey–blue/grey, hard, compact, laminated limestones associated with freshwater plants, ostracods, and brackish/marine encrusting bivalves such as oysters and mussels, indicative of shallow marine conditions with freshwater input and are situated in a relatively small geographic area, reducing potential depositional or post-depositional biases. Herein, the results of chapters 2 and 3 are presented as summaries of taxic composition, abundance, and relative diversity for the English Rhaetian, Hettangian, and Sinemurian, three key assemblages for investigating change in insect diversity across the TJB. Comparisons are also made with contemporaneous assemblages from other countries where possible and the palaeoecology of the British islands at the time is discussed.

4.2 Assemblage composition

4.2.1 The Rhaetian Penarth Assemblage (pre-extinction/extinction fauna)

There are a total of 1133 specimens of insects from the Penarth Group in the British collections. However, around half of these are too fragmentary to identify or were not labelled with a precise locality, so an age could not be determined. There are 68 species, 52 genera, 34 families, and 10 orders represented (Table 4.1). The assemblage consists of cockroaches (Blattodea), beetles (Coleoptera), earwigs (Dermaptera), true flies (Diptera), bugs (Hemiptera), scorpionflies (Mecoptera), lacewings (Neuroptera), dragonflies/damselflies (Odonata), crickets/grasshoppers (Orthoptera), and caddisflies (Trichoptera). There are three relatively diverse localities (Table 4.2), Strensham is the most abundant and speciose followed by Brown's Wood and Aust Cliff. Aust Cliff represents quite different facies to the Severn Valley beds as the insects are found in the Landscape Marble which is peculiar to the area around Bristol. It is discussed separately in a following section.

Table 4.1. Species list for the Lilstock Formation.

Order	Family	Species	Authorship	Locality
Blattodea	Caloblattinidae	*Rhiphidoblattina geikiei*	(Scudder, 1886)	Grey Hill, Browns Wood
	unknown	*Actinoblattula liasina*	(Giebel, 1856)	Strensham
Coleoptera	Carabidae	*Pterostichites grandis*	Horwood, 1916	Glen Parva
	Chrysomelidae	*Chrysomela andraei*	(Giebel, 1856)	Forthampton
	Coptoclavidae	*Holcoptera giebeli*	(Handlirsch, 1907)	Grey Hill, Strensham
		H. pigmentatus	Kelly *et al*. 2017	Browns Wood
		H. schlotheimi	(Giebel, 1856)	Aust, Grey Hill, Brockeridge, Forthampton, Strensham, Wainlode
	Dytiscidae	unknown.		Wainlode
	Elateridae	*Anepismus vanus*	(Giebel, 1856)	Strensham, Wainlode
		Elaterophanes acutus	Cockerell, 1915	Wainlode
		E. vetustus	(Brodie, 1845)	Grey Hill
		Mimelater angulatus	(Giebel, 1856)	Wainlode
		Plastelater neptuni	(Giebel, 1856)	Hasfield
		Stenelytron redtenbacheri	(Giebel, 1856)	Brockeridge, Wainlode
	Gyrinidae	*Paragyrinus dubius*	(Giebel, 1856)	Brockeridge
		Xenogyrinus natans	(Brodie, 1845)	Forthampton
	Cupedidae	*Omma liassicum*	Crowson, 1962	Norton, Hasfield, Browns Wood
	Permosynidae	*Dinoharpalus liasinus*	(Giebel, 1856)	Aust
	unknown	*Ancylocheira liasina*	(Giebel, 1856)	Strensham
		Anhydrophilus brodiei	Handlirsch, 1906	Craycombe, Wainlode
		Bellingera ovalis	Heer, 1852	Aust
		Coleopteron aquaticus	(Brodie, 1845)	Hasfield
		Hydrobiites anglicus	Handlirsch, 1906	Hasfield
		H. giebeli	Handlirsch, 1906	Aust
		H. liasinus	(Giebel, 1856)	Hasfield
		Pseudotelephorus haueri	(Giebel, 1856)	Forthampton
		Stigmenamma heeri	(Giebel, 1856)	Hasfield
Dermaptera	Dermapteridae	*Phanerogramma heeri*	(Giebel, 1856)	Grey Hill, Browns Wood, Forthampton, Norton, Wainlode
Diptera	Chironomidae	*Aenne triassica*	Krzemiński & Jarzembowski, 1999	Aust
	Rhaetaniidae	*Rhaetania dianae*	Krzemiński & Krzemińska, 2002	Strensham
Hemiptera	Archegocimicidae	*Britannicola senilis*	Popov *et al*., 1994	Apperley
	Dysmorphoptilidae	*Dysmorphoptila liasina*	(Giebel, 1856)	Grey Hill, Browns Wood, Wainlode, Garden Cliff
	Hylicellidae	*Homopterites anglicus*	Handlirsch, 1906	Wainlode
	Pachymeridiidae	*Pachymerus zucholdi*	(Giebel, 1856)	Strensham
	Procercopidae	Hem:Proc. sp. nov. 1	Kelly & Ross, in prep. b	Browns Wood
		Hem:Proc. sp. nov. 2	Kelly & Ross, in prep. b	Browns Wood
	Progoninumidae	*Cicadocoris anglicus*	Popov *et al*., 1994	Browns Wood
	Tettigarctidae	*"Liassocicada" ignotus*	(Brodie, 1845)	Forthampton, Hasfield, Strensham
Mecoptera	Bittacidae	*Protobittacus liassicus*	Tillyard, 1933	Strensham
		P. maculatus	Tillyard, 1933	Strensham
	Orthophlebiidae	*Orthophlebia liassica*	(Mantell, 1844)	Grey Hill, Browns Wood, Forthampton, Hasfield, Strensham, Garden Cliff

		O. anglica	(Handlirsch, 1939)	Wainlode
		O. confusa	Willmann, 1977	Forthampton
		O. gracilis	(Handlirsch, 1939)	Strensham
		O. intermedia	(Giebel, 1856)	Strensham
		Protorthophlebia latipennis	Tillyard, 1933	Browns Wood
		Chauliodites minor	(Blake, 1876)	Hotham
	Permochoristidae	*Mesochorista anglicana*	(Tillyard, 1933)	Browns Wood
	Worcestobiidae	*Worcestobia gigantea*	(Tillyard, 1933)	Strensham; Garden Cliff
		W. sp. nov.		
Neuroptera	Mesopolystoecotidae	*Megapolystoechus magnificus*	Tillyard, 1933	Aust, Strensham
	Prohemerobiidae	Neur:Proh. sp. nov. 2	Kelly *et al.*, in prep	Wainlode
Odonata	Liassophlebiidae	*Liassophlebia withersi*	Tillyard, 1925	Strensham
	Triassolestidae	*Progonophlebia woodwardi*	Tillyard, 1925	Strensham
Orthoptera	Bintoniellidae	*Haglopsis brodiei*	Cockerell, 1915	Wainlode
		H. parallela	(Giebel, 1856)	Browns Wood, Forthampton, Strensham, Wainlode
	Elcanidae	*Archelcana liasina*	(Giebel, 1856)	Browns Wood, Wainlode, Charfield, Strensham, Wainlode, Garden Cliff
		Orth:Elc. sp. nov	Kelly & Ross, in prep. c	Strensham
	Haglidae	Orth:Hag. gen. & sp. nov.	Kelly & Ross, in prep d	Strensham
		Hagla gracilis	Giebel, 1856	Forthampton, Strensham
	Locustopseidae	*Locustopsis lacoei*	(Cockerell, 1915)	Strensham
		L. spectablis	(Zeuner, 1942)	Strensham
		Mesolocustopsis constricta	(Zeuner, 1942)	Strensham
		M. gracilis	(Zeuner, 1942)	Strensham
	Protogryllidae	*Protogryllus grandis*	Zeuner, 1937	Strensham
		P. parallelus	Zeuner, 1937	Browns Wood
	unknown	*Liadolocusta auscultans*	Handlirsch, 1907	Forthampton
Trichoptera	Necrotauliidae	*Austaulius furcatus*	(Giebel, 1856)	Aust

Table 4.2. Insect diversity of English Rhaetian localities

Rhaetian localities	Abundance	Species richness
Strensham	149	29
Brown's Wood	132	20
Aust Cliff	110	21
Wainlode Cliff	101	19
Forthampton	57	11
Garden Cliff	52	7
Grey Hill	49	10
Hasfield	27	8
Brockeridge	14	6
Prior's Norton	13	4
Craycombe	7	4
Stoke Gifford	9	1
Tortworth	4	2
Charfield	2	1
Glen Parva	1	1

The English upper Rhaetian is dominated by two orders (Fig. 4.1), Coleoptera with 47% of the total abundance, 37% of species, and 38% of genera in at least 10 families and Orthoptera with 21% of the abundance, 19% of species, and 15% of genera, in five families. Hemiptera account for 13% of the abundance, 12% of species, and 13% of genera which places it third in terms of abundance. However, although Mecoptera only account for 7% of the total abundance, they account for 12% of the species richness and 13% of the genus richness. Odonata account for 3% of abundance (3% species; 4% genera) and Trichoptera account for 4% abundance (1% species; 2% genera). The other four orders (Blattodea, Dermaptera, Diptera, and Neuroptera) account for only 6% of the total abundance, 10% of species, and 16% of genus richness between them.

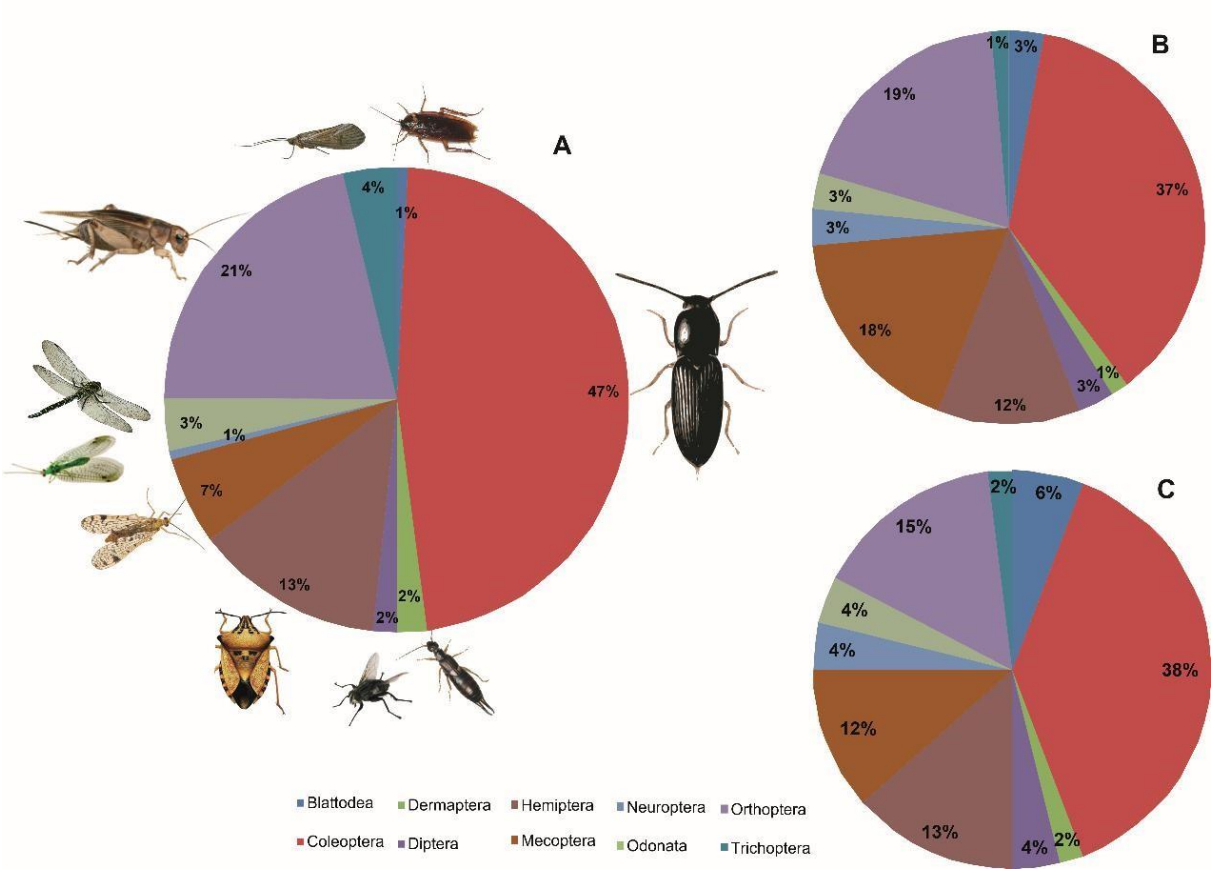

Figure 4.1. British upper Rhaetian relative diversity. A. Abundance; B. Species richness; C. Genus richness.

Landscape Marble.—The Landscape Marble is restricted to the Bristol area and as discussed in Chapter 2 represents a very shallow, lagoonal shelf with an archipelago of small islands throughout and a stromatolitic, reef habitat. This represents markedly different facies to the more laminated, shallow marine with freshwater fluvial input of the Severn Valley where most of the Rhaetian insects are found. The entomofauna is also notably different, with proportionally half the numbers of crickets/grasshoppers and bugs, over four times the proportional abundance of caddisflies, and twice

the proportional abundance of lacewings (Fig. 4.2). This could represent a bias, unevenly promoting the preservation of Trichoptera, but this is unlikely. Caddisfly wings are small and relatively fragile, certainly smaller and more fragile than orthopteran wings and more fragile than hemipteran wings. It may be that this horizon represents a distinct habitat. Aust was relatively cut off from the Welsh Massif (Fig. 2.1) and is probably only sampling the smaller islands around the Bristol area. The deposition site was possibly very close to a shoreline lake, similar to Slapton Ley in Devon, a freshwater lake separated from the English Channel by only a few meters of land. At Slapton Ley caddisflies emerge from the lake en-masse following pupation and head towards the English Channel where many can fall into the water where they can drown in the shallow marine water (personal observation from previous field work). Several of the specimens are well-preserved, more so than those from anywhere else, so a long period of transport is unlikely. This means that they would have entered the water close to the deposition site, rather than travelling through a fluvial system. The caddisflies all seem to be the same species (*Austaulius furcatus*) further suggesting that we are catching an emergence event.

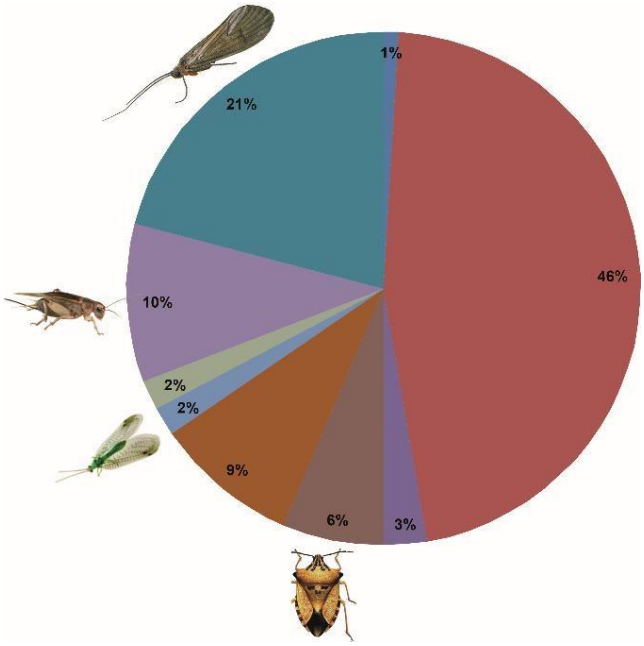

Figure 4.2. Proportional abundance of the Landscape Marble insects from Aust Cliff.

4.2.2 Blue Lias assemblage (recovery fauna)

There are 709 specimens collected from the Blue Lias Formation, mostly from English deposits although two specimens were collected from Cnap Twt quarry in Wales. of these, 201 were not included in the study as they were either too fragmentary to identify or were not labelled with a locality, so an age could not be determined. There are 37 species represented, in 31 genera, 19 families, and nine orders (Table 4.3). The assemblage consists of cockroaches (Blattodea), beetles

(Coleoptera), earwigs (Dermaptera), bugs (Hemiptera), scorpionflies (Mecoptera), lacewings (Neuroptera), dragonflies/damselflies (Odonata), crickets/grasshoppers (Orthoptera), and caddisflies (Trichoptera). Diptera are not recorded from the Hettangian.

Table 4.3. Species list for the Blue Lias Formation.

Order	Family	Species	Authorship	Locality
Blattodea	Mesoblattinidae	*Mesoblattina* sp.		Binton
Coleoptera	Coptoclavidae	*Holcoptera giebeli*	(Handlirsch, 1907)	Binton
		H. schlotheimi	(Giebel, 1856)	Binton, Stratford, Wilmcote
	Cupedidae	*Metacupes harrisi*	Gardiner, 1961	Cnap Twt
	Elateridae	*Elaterophanes vetustus*	(Brodie, 1845)	Binton
	Cupedidae	*Omma liassicum*	Crowson, 1962	Binton
	unknown	*Protocuneus punctatus*	Cockerell, 1915	Wilmcote
	Buprestidae	unknown		Binton
Dermaptera	Dermapteridae	*Phanerogramma heeri*	(Giebel, 1856)	Copt Heath
Hemiptera	Protocoridae	*Protocoris indistinctus*	Popov *et al*., 1994	Binton
	Dysmorphoptilidae	*Dysmorphoptila liasina*	(Giebel, 1856)	
	Belostomatidae	unknown		Binton
	Archijassidae	unknown		Binton
	Tettigarctidae	unknown		Binton
	Cercopidae	unknown	Coram coll'n	Pinhay Bay
Mecoptera	Liassophilidae	*Liassophila hydromanicoides*	Tillyard, 1933	Binton
	Orthophlebiidae	*Orthophlebia liassica*	(Mantell, 1844)	Binton; Grafton
		O. longissima	(Giebel, 1856)	
		O. pictipennis	Tillyard, 1933	Binton
		Mesopanorpa brodiei	Tillyard, 1933	Binton
		Protorthophlebia latipennis	Tillyard, 1933	Binton
Neuroptera	Prohemerobiidae	Neur:Proh. sp. nov. 1	Kelly *et al.*, in prep.	Binton
Odonata	Campterophlebiidae	*Archithemis liassina*	(Strickland, 1840)	Binton
		Petrophlebia anglicana	Tillyard, 1925	Barrow
	Liassophlebiidae	*Liassophlebia magnifica*	Tillyard, 1925	Binton
	Heterophlebiidae	*Heterophlebia buckmani*	Tillyard, 1925	Binton
Orthoptera	Bintoniellidae	*Haglopsis brodiei*	Cockerell, 1915	Binton; Grafton;
		H. parallela	(Giebel, 1856)	Binton Stratford, Nook
	Elcanidae	*Archelcana liasina*	(Giebel, 1856)	Binton, Bidford, Stratford, Wilmcote
		Parelcana anglicana	Handlirsch, 1939	Binton
	Haglidae	Orth:Hag. gen. et sp. nov	Kelly & Ross, in prep. d	Binton
		Hagla gracilis	Giebel, 1856	Binton, Grafton
		Liassophylum abbreviatum	Zeuner, 1935	Binton
	Locustopseidae	*Locustopsis lacoei*	(Cockerell, 1915)	Binton
		L. spectablis	(Zeuner, 1942)	Copt Heath
	Protogryllidae	*Protogryllus magnus*	Zeuner, 1937	Binton
		P. parallelus	Zeuner, 1937	Binton
Trichoptera	Necrotauliidae	*Austaulius furcatus*	(Giebel, 1856)	Copt Heath

A small area of the English Midlands is the most productive place for Lower Hettangian aged insects in the world, with very few other regions represented at this time. Unlike the Rhaetian there is

only one diverse locality, Binton, with 430 specimens (81% of total abundance) collected and 24 species recorded (75% of total species richness), the next most diverse locality is Wilmcote, which is only 4.5 km away from Binton, with 39 specimens (7% of total Hettangian abundance) and eight species (17% of Hettangian species richness).

Table 4.4. Insect diversity of British Hettangian localities

Hettangian Localities	Abundance	Species Richness
Binton	430	24
Wilmcote	39	8
Copt Heath	14	6
Bidford	11	3
Temple Grafton	8	4
Pinhay Bay	6	2
Stratford	5	3
Nook quarry	5	3
Barrow	4	2
Bedminster Down	3	1
Locks Mill, Bristol	3	1
Cnap Twt	2	1

The British Lower Hettangian is dominated in terms of abundance by two orders (Fig. 4.3). Unlike all other assemblages, the most dominant is not Coleoptera, but rather Orthoptera with 43% of the abundance, 30% of the species, and 26% of the genera in five families. Coleoptera accounts for 33% of the abundance and 19% of the species and genera. Mecoptera and Odonata are similarly diverse, accounting for 8% abundance (11% species; 13% genera) and 9% abundance (16% species; 13% genera), respectively. Hemipteran abundance dropped quite a lot from the Rhaetian accounting for only 4% of Hettangian abundance, but the relative species richness is 14% and genus richness 16%, similar to Rhaetian levels. The remaining four orders (Blattodea, Dermaptera, Neuroptera, and Trichoptera) account for only 12% of species and genera and only 4% of abundance between them.

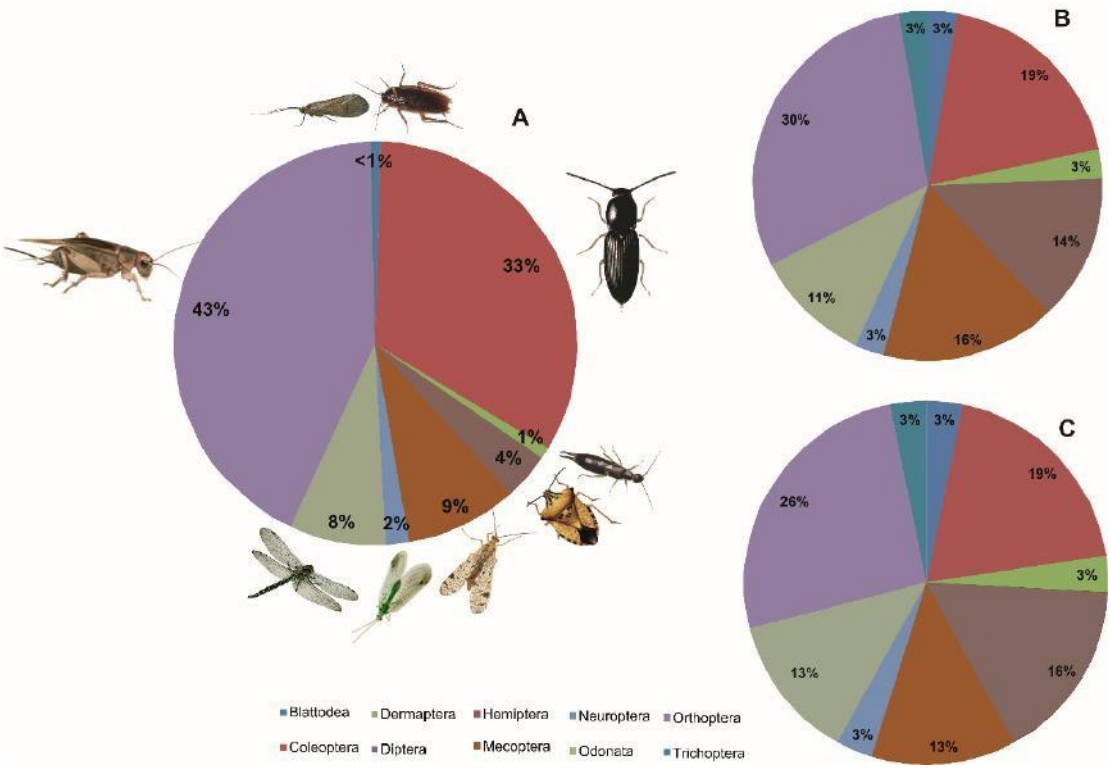

Figure 4.3. British Lower Hettangian relative diversity. A. Abundance; B. Species richness; C. Genus richness.

4.2.3 Charmouth Mudstone assemblage (post-extinction fauna)

Abundant insects have been collected from the English Sinemurian from five localities along the Jurassic Coast of England (Table 4.5). There are 710 specimens in the registered collections that were examined for the project and a further 570 specimens from private collections. There are 61 species, 48 genera, 39 families, and 13 orders represented. The assemblage comprises cockroaches (Blattodea), beetles (Coleoptera), earwigs (Dermaptera), true flies (Diptera), bugs (Hemiptera), moths (Lepidoptera), scorpionflies (Mecoptera), lacewings (Neuroptera), dragonflies/damselflies (Odonata), crickets/grasshoppers (Orthoptera), stick insects (Phasmatodea), snakeflies (Raphidioptera), and caddisflies (Trichoptera).

Table 4.5. Insect diversity of English Sinemurian localities

Sinemurian localities	Abundance	Species richness
Stonebarrow (Obtusum)	208	41
Black Ven (Obtusum)	182	33
Catherston Lane (Obtusum)	44	9
Monmouth Beach	221	33
Black Ven (Turneri)	131	21
Stonebarrow (Turneri)	3	1
Western English Channel	2	1
Catherston Lane (Turneri)	1	1

There are several insect-bearing horizons known from both the lower and Upper Sinemurian. 489 specimens have been collected from the Lower Sinemurian and 785 from the Upper Sinemurian. There are 32 species, 23 genera, 22 families, and 11 orders identified from the Lower Sinemurian beds (Table 4.6). Then there are 43 species, 39 genera, 27 families, and 11 orders recorded form the Upper Sinemurian (Table 4.7). Most of the Upper Sinemurian material is from the Jackson collection, much of which has been published previously (Zeuner, 1962; Whalley, 1985; Popov et al., 1994; Ross, 2010). Whereas, most of the Lower Sinemurian material is from private collections.

Table 4.6. Species list for the Lower Sinemurian of England

Order	**Family**	**Species**	**Authorship**	**Locality**
Blattodea	unknown	unknown	Carroll coll'n	Black Ven
Coleoptera	Coptoclavidae	*Holcoptera giebeli*	(Handlirsch, 1907)	Monmouth
		H. schlotheimi	(Giebel, 1856)	Black Ven
		H. alisonae	Kelly *et al*., 2017	Black Ven, Monmouth
	Gyrinidae	unknown	Carroll coll'n	Black Ven
	Cupedidae	*Liassocupes parvus*	Carroll coll'n	Black Ven
		Liassocupes maculatus	Carroll coll'n	Black Ven
		Liassocupes sp	Carroll coll'n	Black Ven
	Staphylinidae	unknown	Carrol coll'n	Monmouth
Dermaptera	Protodiplatyidae	*Brevicula gradus*	Whalley, 1985	Monmouth
		B. maculata	Kelly *et al*., 2018a	Monmouth
Diptera	Anisopodidae	*Megarhyphus amberae*	Krzemińska *et al*., 2010	Monmouth
	Tanyderidae	*Nannotanyderus oliviae*	Skibińska *et al*., 2014	Monmouth
Hemiptera	Tettigarctidae	*Shuraboprosbole rotruda*	Carroll coll'n	Black Ven
	Belostomatidae	*Tarsabedus* sp	Carroll coll'n	Monmouth
	Dysmorphoptilidae	*Dysmorphoptila* sp	Carroll coll'n	Monmouth
	Pterocimicidae	*Pterocimex*	Carroll coll'n	Black Ven
	Fulgoridiidae	unknown	Coram coll'n	Monmouth
Lepidoptera	Archaeolepiidae	*Archaeolepis mane*	Whalley, 1985	Black Ven
Mecoptera	Eomeropidae	*Jurachorista bashkuevi*	Soszyńska-Maj *et al.*, 2016	Monmouth
	Orthophlebiidae	*Orthophlebia liassica*	(Mantell, 1844)	Monmouth
		Protorthophlebia latipennis	Carroll coll'n	Black Ven
Neuroptera	Prohemerobiidae	*Prohemerobius Neur:Proh.sp.nov.3*	Coram coll'n	Monmouth
		P. Neur:Proh.sp.nov.4	Coram coll'n	Monmouth
		Actinophlebia sp	Carroll coll'n	Black Ven
Odonata	Protomyrmeleontidae	*Protomyrmeleon* sp	Carroll coll'n	Monmouth
	Liassophlebiidae	*Liassophlebia* sp	Carroll coll'n	Black Ven
Orthoptera	Bintoniellidae	*Haglopsis parallela*	(Giebel, 1856)	English Channel
	Regiatidae	*Micromacula sp.*	Whalley, 1985	Black Ven

		Regiata sp.	Carroll coll'n	Monmouth
	Protogryllidae	*Protogryllus magnus*	Carroll coll'n	Black Ven
Trichoptera	Necrotauliidae	*Austaulius haustrum*	Kelly *et al*, 2018b	Monmouth

Table 4.7. Species list for the Upper Sinemurian of England.

Order	**Family**	**Species**	**Authorship**	**Locality**
Blattodea	unknown	gen. & p. nov (cockroach)	To be described	Stonebarrow
		gen. nov. *petulantia*	To be described	Stonebarrow
Coleoptera	Coptoclavidae	*Holcoptera alisonae*	Kelly *et al.*, 2017	Black Ven, Stonebarrow, Catherston
		H. giebeli	(Handlirsch, 1907)	Black Ven, Stonebarrow, Catherston
		H. schlotheimi	(Giebel, 1856)	Black Ven
	Elateridae	*Elaterina liassica*	Gardiner, 1961	Black Ven
		Elaterophanes regius	Whalley, 1985	Black Ven, Stonebarrow
	Cupedidae	*Liassocupes maculatus*	(Whalley, 1985)	Stonebarrow
		L. parvus	Whalley, 1985	Black Ven, Catherston
		Omma liassicum	Crowson, 1962	Stonebarrow
	Schizophoridae	*Mimemala giganteum*	(Whalley, 1985)	Stonebarrow
		Tersus crowsoni	Ponomarenko, 2006	Stonebarrow
Dermaptera	Protodiplatyidae	*Brevicula gradus*	Whalley, 1985	Black Ven
Diptera	Oligophrynidae	*Oligophryne britannica*	Ansorge & Krzemiński, 1994	Stonebarrow
	Ptychopteridae	*Eoptychoptera spectra*	(Whalley, 1985)	Stonebarrow
Hemiptera	Belostomatidae	*Lethonectes naucoroides*	Popov *et al*., 1994	Stonebarrow
		Tarsabedus menkei	Popov *et al*., 1994	Stonebarrow
	Corixidae	*Liassocorixa dorsetica*	Popov *et al*., 1994	Black Ven, Stonebarrow
	Hylicellidae	*Mesocixiella fennahi*	Whalley, 1985	Stonebarrow
	Ochteridae	*Propreocoris maculatus*	Popov *et al*., 1994	Black Ven
	Pachymeridiidae	*Neomeridium trifurcum*	Popov *et al*., 1994	Black Ven, Stonebarrow
	Pterocimicidae	*Pterocimex jacksoni*	Popov *et al*., 1994	Black Ven, Stonebarrow
	Tettigarctidae	*Shuraboprosbole rotruda*	(Whalley, 1985)	Black Ven, Stonebarrow
Mecoptera	Orthophlebiidae	*Orthophlebia capillata*	Whalley, 1985	Black Ven, Stonebarrow
		Protorthophlebia latipennis	Tillyard, 1933	Stonebarrow
	Bittacidae	*Protobittacus* sp	Carroll coll'n	Black Ven

	Pseudopolycentropodidae	*Pseudopolycentropus triangularis*	Handlirsch, 1920	Black Ven
Odonata	Anglophlebiidae	*Anglophlebia gigantea*	(Zeuner, 1962)	Stonebarrow
	Campterophlebiidae	*Dorsettia laeta*	Whalley, 1985	Stonebarrow
		Hypsothemis fraseri	Whalley, 1985	Stonebarrow
		Lateophlebia anglicanopsis	(Zeuner, 1962)	Stonebarrow
	Liassophlebiidae	*Liassophlebia pseudomagnifica*	Whalley, 1985	Black Ven
		Rossiphlebia jacksoni	(Zeuner, 1962)	Catherston, Stonebarrow
Orthoptera	Elcanidae	*Archelcana liasina*	(Giebel, 1856)	Black Ven, Stonebarrow
	Haglidae	*Protohagla langi*	Zeuner, 1962	Stonebarrow
	Locustopseidae	*Orth:Loc. sp. nov.*	Kelly & Ross (*In prod. a*)	Black Ven
		Locustopsis ornatum	(Whalley, 1985)	Black Ven
	Protogryllidae	*Protogryllus magnus*	Zeuner, 1937	Black Ven, Catherston
	Regiatidae	*Micromacula gracilis*	Whalley, 1985	Black Ven, Stonebarrow
		Regiata scutra	Whalley, 1985	Black Ven, Stonebarrow
Phasmatodea	Aerophasmidae	*Durnovaria parallela*	Whalley, 1985	Stonebarrow
Raphidioptera	Mesoraphidiidae	*Mesoraphidia confusa*	(Whalley, 1985)	Black Ven
	Priscaenigmatidae	*Priscaenigma obtusa*	Whalley, 1985	Black Ven

Carroll and Coram collections.—Two private collections from the Dorset Coast were surveyed for the present study, some specimens of newly discovered species were donated and described, but the majority of the material remains in need of description. All insects were identified to at least family or genus level where possible and included in the diversity analysis for Chapter 5. These collections are important as they mostly comprise Lower Sinemurian insects; whereas, the Jackson collection mostly comprises Upper Sinemurian insects. There are at least 200 from the Coram collection and 380 from the Carroll collection representing, beetles (including, *Holcoptera giebeli* and *H. alisonae*), odonates (including *Liassophlebia*), lacewings, caddisflies, snakeflies, flies, scorpionflies (including, *Probittacus*, *Liassochorista*, *Orthophlebia* sp., and one *Orthophlebia liassica*), orthopterans (including, locustopseids and regiatids), and numerous bugs. The Carroll collection also include the only three known Pliensbachian insects from Britain, from Golden Cap.

The English Sinemurian is dominated in both the lower and upper parts by Coleoptera (Figs 4.4, 4.5), which account for 47% of total abundance in the lower beds, and 51% in the upper beds. The species and genus richness are much lower, but this is probably because most have not been taxonomically worked on yet. In the Lower Sinemurian the second most abundant are Hemiptera which account for 21% of the total abundance, 21% of species and 19% of genera, but in the upper beds, although the order only accounts for 11% of the total abundance, it also represents 17% of

species and 20% of genus richness. Orthoptera are more dominant in the upper beds accounting for 27% of the total abundance (22% species, 18% genus richness), whereas this order accounts for 13% of abundance in the lower part. Diptera are relatively abundant in the Lower Sinemurian accounting for 7% of the abundance (10% species; 13% genera); whereas, in the Upper Sinemurian Diptera accounts for <1% of abundance (2% species, 3% genus richness).

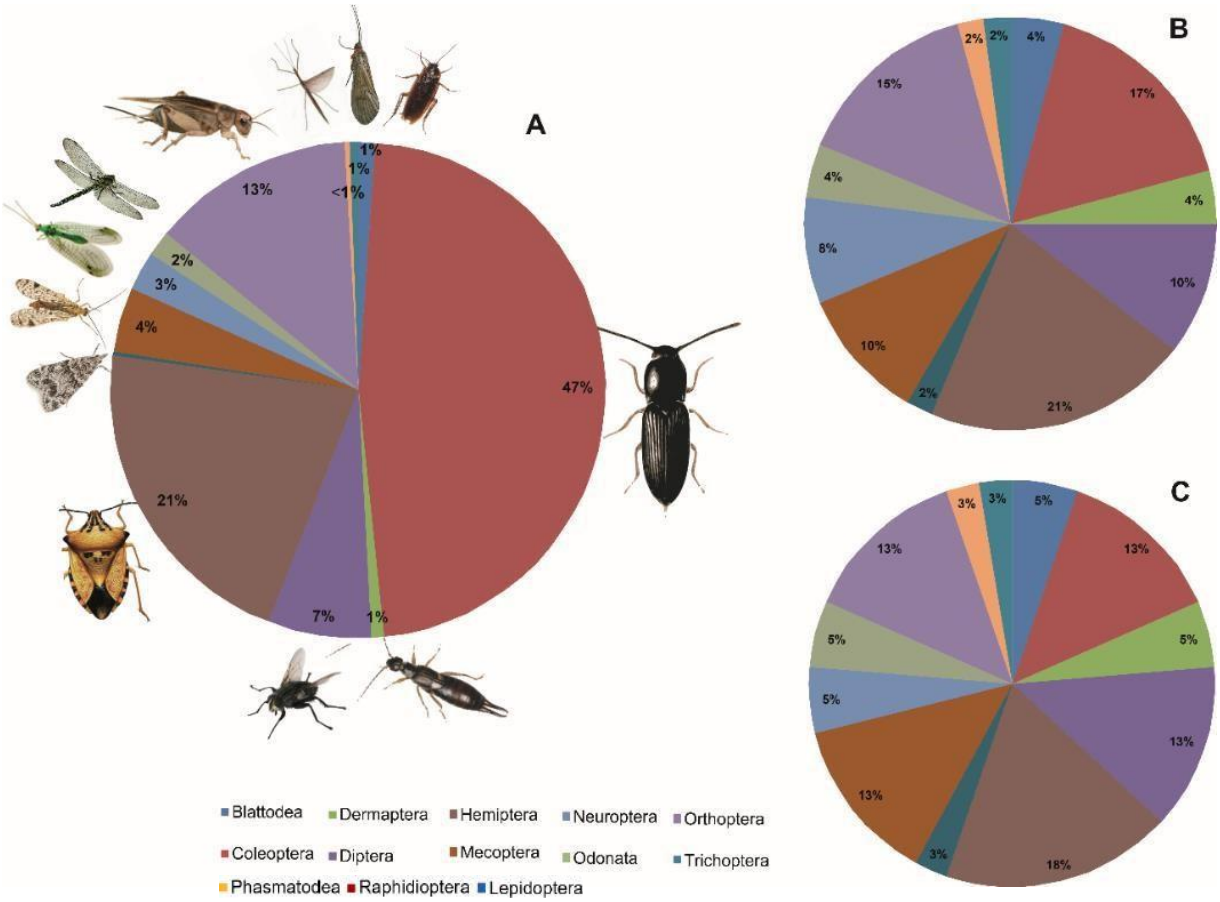

Figure 4.4. British Lower Sinemurian relative diversity. A. Abundance; B. Species richness; C. Genus richness.

Mecoptera are quite stable between the lower and upper beds accounting for 4% of the abundance in each, but with a slight drop in proportional richness in the upper beds. Odonata accounts for 2% (4% species; 5% genera) in the lower beds, doubling to 4% I the upper beds with 13% of the species and genera. Dermaptera 1% in both the lower and upper beds (lower: 4% species, 5% genus richness; upper: 2% species; 3% genera). Neuroptera 3% in the lower (8% species; 5% genera), dropping to <1% in the upper beds (2% species, 3% genus richness).

Raphidioptera and Lepidoptera are not known from the Rhaetian or Hettangian of the UK, the former accounts for <1% of the abundance in upper beds (4% species, 5% genus richness); the latter is only known from the lower beds and accounts for <1% of the abundance (2% species, 3% genus richness). Blattodea are relatively rare in both the lower and upper beds, with only 1% of the abundance (4% species; 5% genera) in the lower beds and 2% of the abundance (4% species; 5%

genera) in the upper beds. Phasmatodea are not known from the Rhaetian or Hettangian of the UK, they are only known from the Sinemurian and account for <1% of the abundance (2% species; 3% of genera) in both the upper and lower beds.

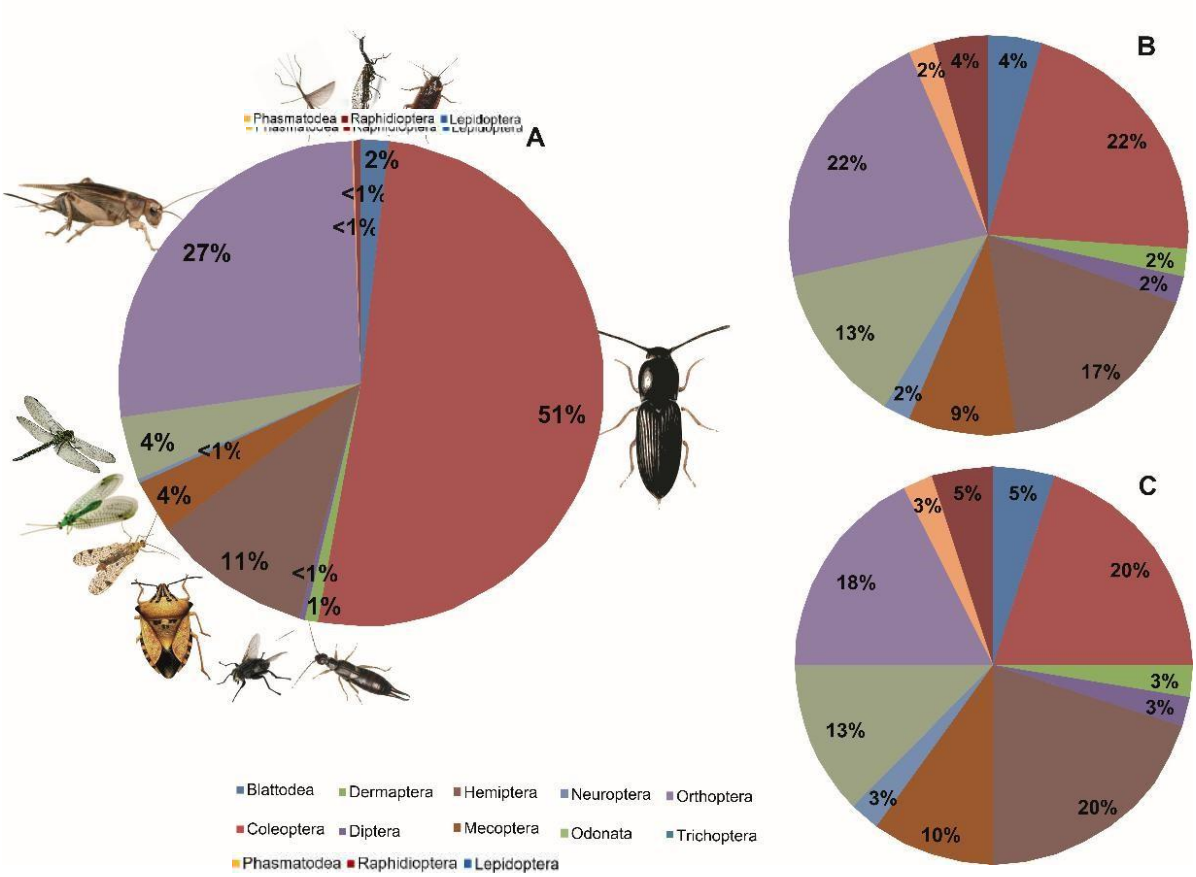

Figure 4.5. British Upper Sinemurian relative diversity. A. Abundance; B. Species richness; C. Genus richness.

4.3 COLEOPTERA

There are 353 beetles from the Lilstock Formation, only 77 of which have been described to at least family level, and 177 from the Hettangian, of which 43 are identified to at least family level, and 395 from the Charmouth Mudstone Fm. (168 lower; 227 upper), of which 123 have been identified to at least family level. The majority of the English Late Triassic to Early Jurassic beetles remain undescribed as it is a difficult order to work with taxonomically, owing to the fact that isolated elytra do not generally preserve the same levels of taxonomic data as the isolated forewings of other orders with phylogenetically informative venation patterns. Unless a beetle elytron is particularly distinctive (e.g. *Holcoptera*, see Kelly et al., 2017) then it is difficult to classify them to genus or species level.

The most abundant family in the Rhaetian, Hettangian, and Sinemurian is Coptoclavidae. There are 20 specimens representing three species in the dataset, *Holcoptera schlotheimi*, *H. giebeli*, and *H. pigmentatus* from the Rhaetian, 28 specimens representing two species, *Holcoptera giebeli* and *H.*

schlotheimi, from the Hettangian, and 111 specimens, representing three species, *H. giebeli*, *H. schlotheimi*, and *H. alisonae* from the Sinemurian (31 lower; 80 upper). There is one earlier species in the dataset known from the Norian Cow Branch Formation of the US, *H. solitensis*. *H. pigmentatus* is known from a single specimen from the Lilstock Formation and appears to have gone extinct before the Lower Hettangian. *H. schlotheimi* and *H. giebeli* are recorded in both the Rhaetian and Hettangian. *H. schlotheimi* was relatively abundant in the English Rhaetian whereas there is only one known specimen of *H. giebeli*. Following the TJB, however, both species increase in abundance with *H. schlotheimi* more prevalent in the English and US Hettangian, and potentially the US Sinemurian and *H. giebeli* becoming dominant in the English Sinemurian, when we also see the appearance of *H. alisonae* which is known only from the English Sinemurian. The genus is not known from deposits younger than the Sinemurian, including the extremely productive Lower Toarcian German deposits, and so probably went extinct between the Upper Sinemurian and Lower Toarcian.

The family is relatively well distributed in the dataset (Fig. 4.6), also being found in the Carnian Huangshanjie Formation of China and the Hassberge Formation of Germany, the Toarcian Posidonia Shale Formation of Germany and Cheremkhovo Formation of Russia, and the Early Jurassic Sagul Formation of Kyrgyzstan. There may be additional specimens of *Holcoptera* from the Upper Carnian Hassberge Formation of Germany (*Stargelytron* of Ponomarenko et al., 2015), the Norian Argilliti di Riva di Solto Formation of Italy (Whalley, 1988), and some undescribed material from the Lower Sinemurian Badaowan Formation of China (personal observation of collections at NIGPAS) but these require further examination.

There are a number of extant families recorded in the dataset: Cupedidae, Elateridae, Buprestidae, Gyrinidae, Cantharidae (=Telephoridae), Hydrophilidae, Dytiscidae, Chrysomelidae, and Carabidae, as well as one extant genus, *Omma*. These identifications, however, are often based on isolated elytra which are difficult to identify to extant taxa as they often require antennal and tarsal (leg) formulas and other non-preserved morphological characters to identify accurately. There are several families in the Rhaetian which are not present in the Early Jurassic of the UK (Carabidae, Chrysomelidae, and Gyrinidae) but these families are extant and so may have gone extinct locally and then returned following the Hettangian. Two specimens of Cupedidae are the only specimens known from the Triassic/Jurassic of Wales, both identified as *Metacupes harrisi*. This genus is endemic to Wales. Cupedidae is also found in the Pliensbachian Makarova Formation of Russia. There is one specimen of the extant genus Cupedidae: *Omma* in the dataset, described as *O. liassicum*. The genus is also found in the Sinemurian Dzhil Formation of Kyrgyzstan. The family is also found in the Hettangian Zagaje Formation of Poland, the Hettangian Guanyintan Formation (Paijiachong Member) of China, the Pliensbachian Sulyukta Formation of Tajikistan, and the Sinemurian–Toarcian Cattamarra Coal Measures of Australia.

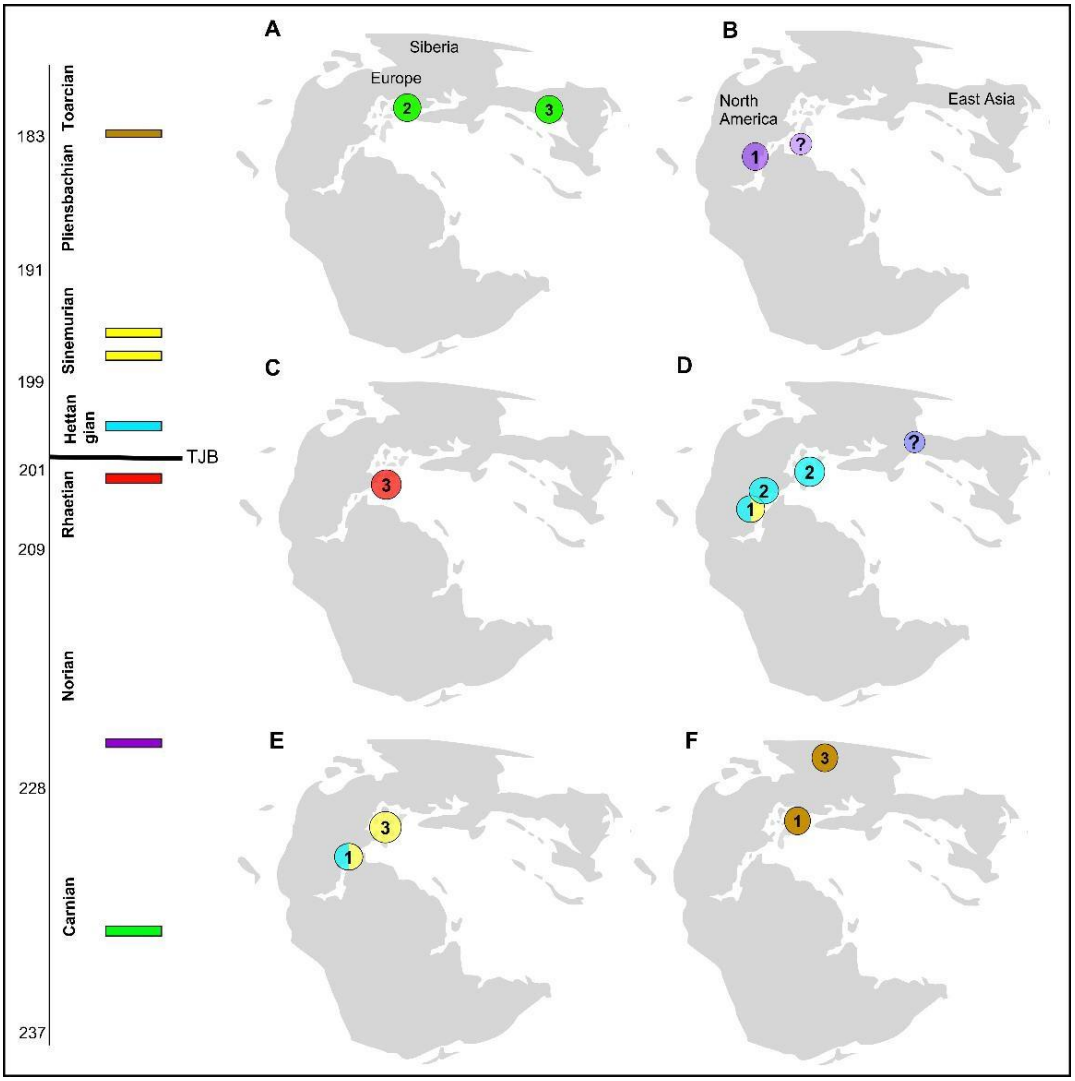

Figure 4.6. Global distribution of the beetle family Coptoclavidae in the Late Triassic and Early Jurassic. A. Carnian, B. Norian, C. Rhaetian, D. Hettangian, E. Sinemurian, F. Toarcian. Circles coloured by age on timeline to the left; numbers represent species richness. '?' for unconfirmed records from Italy and China.

4.4 Orthoptera

There are 145 specimens identified as orthopterans (crickets and grasshoppers) from the Rhaetian, with 88 identified to at least family level, 226 specimens from the Hettangian, 67 of which are identifiable to at least family level, and 165 from the Sinemurian (47 lower; 118 upper), 56 of which are identified to at least family level. The vast majority belong to the suborder Ensifera (crickets) with representatives of the families: Bintoniellidae, Haglidae, and Protogryllidae. Elcanidae is also represented, a family with characteristics of both Ensifera (antennae longer than their bodies) and Caelifera (simple wings without any stridulatory apparatus), so they remain of unsure taxonomic position (Fang et al., 2018) but are usually considered in Ensifera (e.g. Gorochov et al., 2006). The

remaining specimens belong to the suborder Caelifera (grasshoppers) which is represented by two families, Locustopseidae and Regiatidae.

The most abundant family in the Rhaetian is Bintoniellidae with 30 specimens (4% of total abundance; 21% of orthopterans) but with rather low generic and species richness, with only one genus and two species recorded. One of those species (*Haglopsis parallela*) is dominant, with 25 specimens, the other (*Haglopsis brodiei*) has only one specimen, and three are only identified to family level. The family is more abundant in the Hettangian, but is not the most abundant, with 52 specimens (10% of total abundance; 23% of orthopterans) of the same two species found in the Rhaetian, but *H. brodiei* is slightly more abundant (25 specimens) than *H. parallela* (19 specimens). The family is not known from the abundant collections from the Sinemurian of the south coast, the only known Sinemurian aged representatives of this family is one specimen of *H. parallela* collected during borehole drilling in the Western English Channel (Whalley, 1982). Both of these species are endemic to England in the Triassic and Jurassic. The dataset suggests that the family had a geographic range which spread to at least Central Asia in the Late Triassic, also being found in the Carnian Madygen Formation of Kyrgyzstan, but it has not been recorded anywhere else in the Early Jurassic.

Elcanidae is the most abundant family in the Hettangian with a slightly higher abundance than Bintoniellidae (58 specimens, 11% of total abundance, 25% of orthopterans) and is represented by two genera and species, *Archelcana liasina* and *Parelcana anglicana*. It was much less abundant before this in the Rhaetian and after in the Sinemurian. There are 12 specimens known from the Rhaetian (1.5% of total abundance, 8% of orthopterans), with two species identified, *A. liasina* and "Orth:Elc. sp. nov.". There are 16 specimens known from the Upper Sinemurian (3.5% of total abundance, 10% of orthopterans), with only one species, *A. liasina*, identified. Another species, *Parelcana dubia*, is recorded from "Gloucestershire", but as this locality is not precise it is not possible to ascertain its age. All species are endemic to England in the Triassic and Jurassic, but *Archelcana* has a wider distribution in the dataset, also being found in the Norian Arnstadt Formation of Germany, the Pliensbachian/Toarcian Sagul Formation of Kyrgyzstan, and the Toarcian Cheremkhovo Formation of Russia, but it is more diverse in England with only one species recorded in each of these other formations. *Parelcana* is endemic to Europe, also being found in the Toarcian Posidonia Formation of Germany. The family is also found in the Hettangian Staffeleg Formation of Switzerland.

There are 21 specimens identified as Haglidae from the Rhaetian (3% of total abundance; 14% of orthopterans) with two genera and species found in the dataset. One species (*Hagla gracilis*) is dominant, with 19 specimens, and one ("Orth:Hag. gen. et sp. nov.") is rare with only one specimen identified. The family is much less abundant in the Hettangian (seven specimens; 1.5% of total abundance; 3% of orthopterans), but more speciose with three species recorded in three genera, the two from the Rhaetian and *Liassophyllum abbreviatum*. The family is even less abundant in the Upper Sinemurian with only four specimens known (<1% of total abundance; 3% of orthopterans), but it is

relatively diverse, with two genera and species identified, *H. gracilis* and *Protohagla langi*. There are none yet identified from the Lower Sinemurian material.

All haglid genera are endemic to England in both the Rhaetian and Hettangian, but the family is widespread and diverse in the dataset (Fig. 4.7), also being found in the Carnian Madygen Formation of Kyrgyzstan in great numbers, but also from the Late Triassic Koldzat and Tologoi formations of Kazakhstan. It is also found in the Carnian Cacheuta Formation of Argentina, the Carnian/Norian Molteno Formation of South Africa/Lesotho, and the Norian Mount Crosby Formation of Australia. Most genera are endemic, except for one genus (*Voliopus*), which is also found in the Madygen and Molteno formations. In the Early Jurassic it is also found in the Hettangian Badaowan Formation of China, an unknown formation estimated as Early Jurassic of China, the Sinemurian Dzhil Formation and the Pliensbachian/Toarcian Sagul Formation of Kyrgyzstan, the Pliensbachian Sulyukta Formation of Tajikistan, and the Toarcian Cheremkhovo Formation of Russia.

There are only five specimens of Protogryllidae from the Rhaetian with two species identified in one genus, *Protogryllus grandis* and *P. parallelus*, and three from the Hettangian with two species recorded, *P. parallelus* and *P. magnus*. Then there are two specimens from the Sinemurian, one is identified as *P. magnus* and the other as ?*Protogryllus* sp. only. There is an additional species described from the Toarcian of Gloucestershire, *P. acutipennis* Handlirsch, 1920 which is also known from the Posidonia Shale Formation of Germany. The only other Late Triassic entry for this family or genus in the dataset is in the Cave Sandstone Formation of South Africa.

Regiatidae is first recorded in the Lower Sinemurian, seven specimens are known (mostly from the Carroll collection), although only the one from the Jackson collection has been identified to species level as *Micromacula gracilis*. There are 10 specimens from the Upper Sinemurian, mostly from the Jackson collection but with two from the Carroll collection. There are two species known from these younger beds, *M. gracilis* and *Regiata scutra*. There is only one additional entry for this family in the dataset, *Protochaeta lanceolata* from the Toarcian Posidonia Shale Formation of Germany.

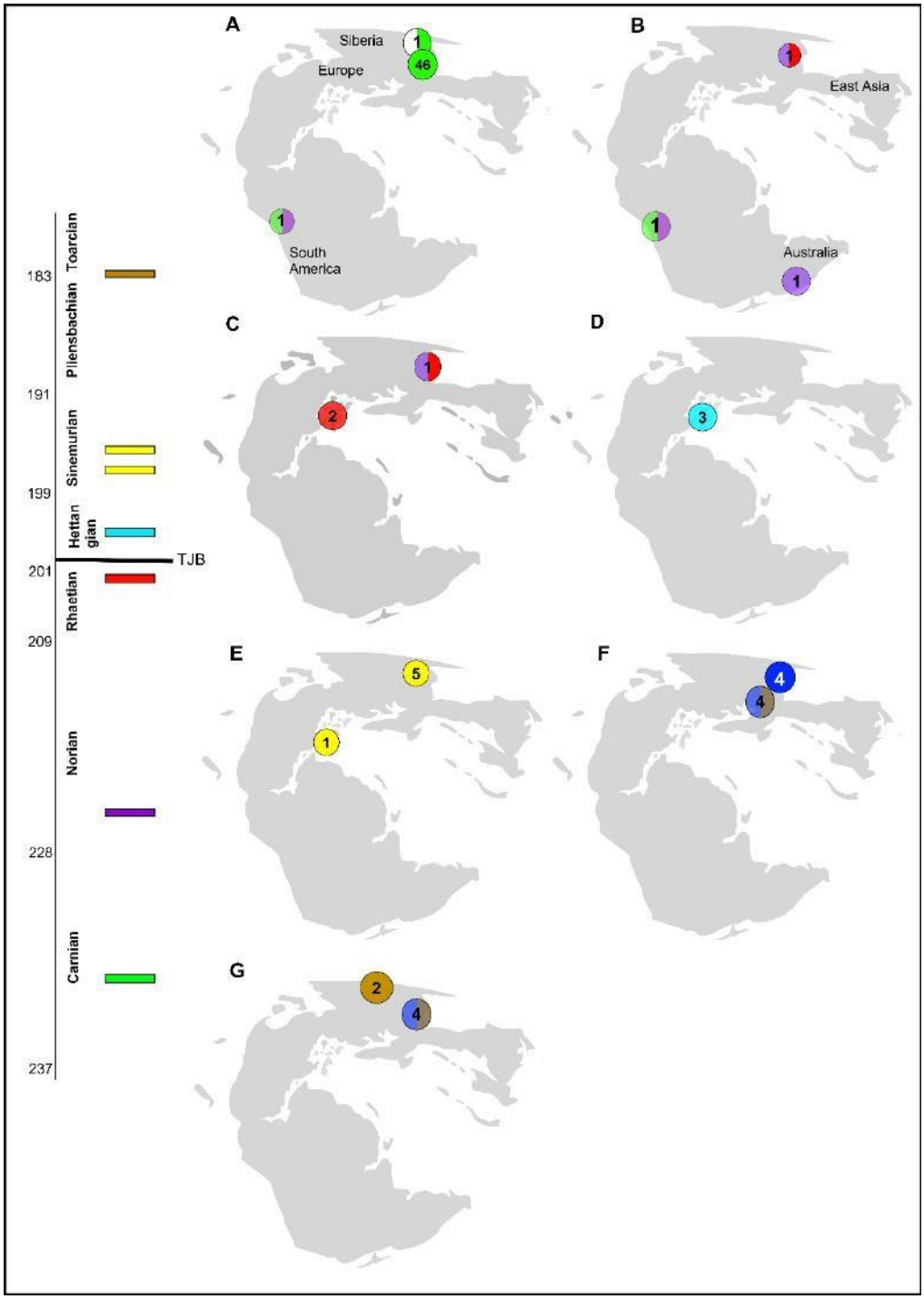

Figure 4.7. Global distribution of the cricket family Haglidae in the Late Triassic and Early Jurassic. A. Carnian, B. Norian, C. Rhaetian, D. Hettangian, E. Sinemurian, F. Pliensbachian, G. Toarcian. Circles coloured by age on timeline to the left; numbers represent species richness.

There are 17 specimens of Locustopseidae identified from the Rhaetian (2.5% of total abundance; 12% of orthopterans), with two genera and four species described. The most abundant is *Locustopsis lacoei* with six specimens; also found are *L. spectablis, Mesolocustopsis constricta,* and *M. gracilis*. The family is much less abundant in the Hettangian (seven specimens, 1% of total abundance; 3% of orthopterans) and only two species in one genus are found: *L. lacoei* and *L. spectablis*. The family

returns to Rhaetian levels of abundance in the Sinemurian, with 15 specimens known (3% of total abundance; 13% of orthopterans). There are two species identified in the Sinemurian, both of which are not known from the earlier deposits, *L. ornatum* and "Orth:Loc. sp. nov.".

Mesolocustopsis is endemic to England in the Late Triassic and Early Jurassic but is also known from the Cretaceous of China (Hong and Wang, 1990) and England (Sukacheva and Jarzembowski, 2001). *Locustopsis* is endemic to England in the Late Triassic but is much more widespread in the Early Jurassic (Fig. 4.8), also being found in the Toarcian Posidonia Shale Formation of Germany, the Pliensbachian Sulyukta Formation of Tajikistan, and the Sinemurian Dzhil and Pliensbachian/ Toarcian Sagul formations of Kyrgyzstan. The family is also found in the Hettangian Staffeleg Formation of Switzerland and the Toarcian Cheremkhovo Formation of Russia.

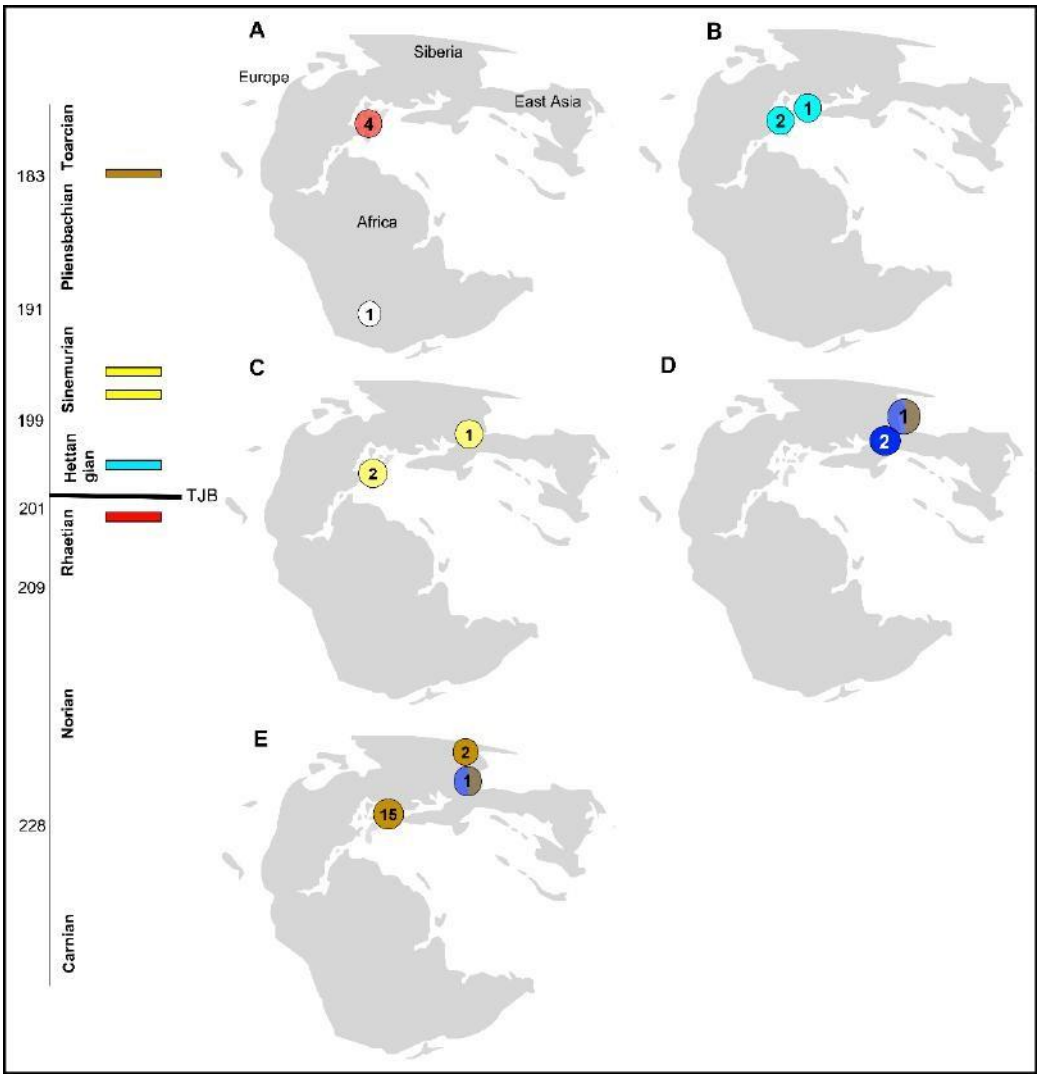

Figure 4.8. Global Late Triassic/Early Jurassic distribution of the grasshopper family Locustopseidae. A. Rhaetian, B. Hettangian, C. Sinemurian, D. Pliensbachian, E. Toarcian. Circles coloured by age on timeline to the left; numbers represent species richness.

4.5 MECOPTERA

There are 53 specimens identified as mecopterans (scorpionflies) from the English Rhaetian, all of which are identified to at least family level. There are 47 from the English Hettangian, only one of which is not identifiable to at least family level. There are 16 specimens from the Upper Sinemurian and 15 from the Lower Sinemurian, all except seven of which are identifiable to at least family level. Orthophlebiidae is by far dominant in most assemblages (Rhaetian: 47 specimens, 6.5% of total abundance, 89% of mecopterans; Hettangian: 45 specimens, 8.5% of total abundance, 95% of mecopterans; Upper Sinemurian: 14 specimens, 3% of total abundance, 93% of mecopterans). However, in the Lower Sinemurian there are three orthophlebiids and four identified as Permochoristidae.

Orthophlebia liassica is the most dominant species in the older assemblages with 36 specimens in the Rhaetian and 32 in the Hettangian, but there is only one specimen from the Lower Sinemurian, and it is not known from the Upper Sinemurian. There are a further four species recorded from the Rhaetian (*O. anglica, O. confusa, O. gracilis, and O. intermedia*) and two different species from the Hettangian (*O. longissimi and O. pictipennis*), but these are currently under revision (e.g. Soszyńska Maj et al, 2017) and are expected to reduce in number as this research progresses. There is one other genus and species recorded, *Protorthophlebia latipennis* which is rare in the older deposits, known only from one specimen in both the Rhaetian and Hettangian, but is more abundant in younger deposits also being known from six specimens in the Sinemurian. *O. liassica* is endemic to England in the Late Triassic and Early Jurassic but *Mesopanorpa brodiei* and *O. brodiei* are also found in the Sinemurian Badaowan Formation of China. The dataset suggests that *Orthophlebia* had a relatively broad distribution in the Late Triassic (Fig. 4.9) as it is also found in the Madygen Formation of Kyrgyzstan, but is even more widespread in the Early Jurassic, also being found in the Sinemurian Badaowan Formation of China and Dzhil Formation of Kyrgyzstan; the Pliensbachian Makarova Formation of Russia and Sulyukta Formation of Tajikistan; the Toarcian Whitby Mudstone Formation of England, Posidonia Shale Formation of Germany, and Cheremkhovo Formation of Russia; and the Early Jurassic Kushmurun Formation of Kazakhstan. The family is additionally known from the Carnian Huangshanjie Formation of China.

Also recorded are, Worcestobiidae, with two specimens from the English Rhaetian representing one species, *Worcestobia gigantea* and another one representing a possible new species in the same genus; Bittacidae, with two specimens from the Rhaetian representing two species, *Probittacus maculatus* and *P. liassica*. Although this family is not known from the Hettangian or Sinemurian, it does reappear in Toarcian represented by *P. handlirschi*. Permochoristidae is also known from one specimen from the Rhaetian representing *Mesochorista anglicana*. One specimen from the Lower Sinemurian represents a family not found in any other British TJB deposit, Eomeropidae, represented by *Jurachorista bashkuevi* from the Coram Collection. All of these species are endemic to England in the Triassic.

Worcestobia is also known from the Carnian Momonoki Formation of Japan. *Probittacus* is endemic to England in the Triassic but Bittacidae is widespread and diverse, also being found in the Norian Mount Crosby Formation of Australia, the Sinemurian Dzhil Formation of Kyrgyzstan, the Pliensbachian Osinovo Formation of Russia and Sulyukta Formation of Tajikistan, the Pliensbachian/ Toarcian Sagul Formation of Kyrgyzstan, and the Toarcian Posidonia Shale Formation of Germany. Permochoristidae is only known from England in the Rhaetian but is also known from the Carnian Potrerillos and Cacheuta formations of Argentina, Madygen Formation of Kyrgyzstan, and Huangshanjie Formation of China; the Norian Blackstone and Mount Crosby formations of Australia; the Norian/Rhaetian Tologoi Formation of Kazakhstan; the Sinemurian Dzhil Formation of Kyrgyzstan; and the Toarcian Posidonia Shale Formation of Germany.

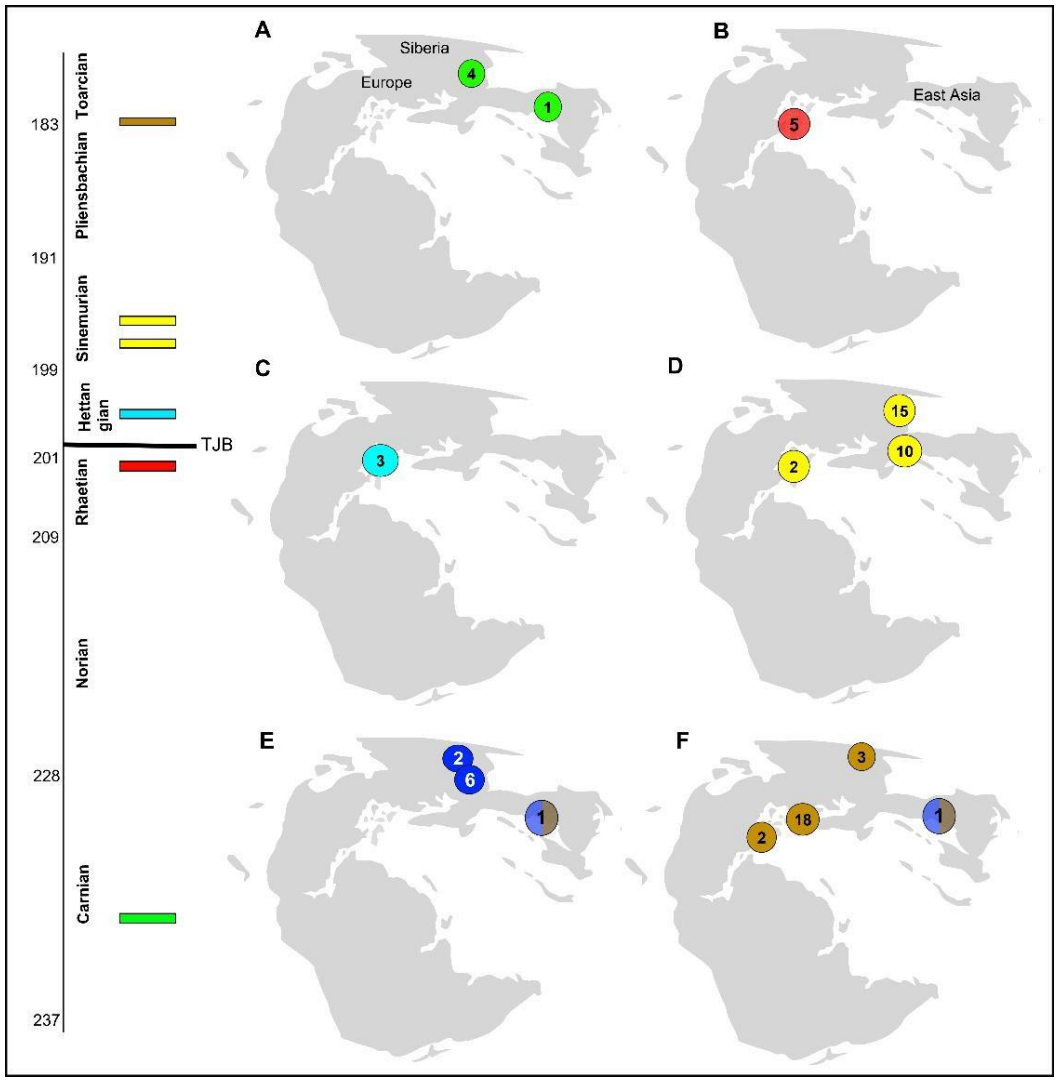

Figure 4.9. Global Late Triassic/Early Jurassic distribution of the scorpionfly family Orthophlebiidae. A. Carnian, B. Rhaetian, C. Hettangian, D. Sinemurian, E. Pliensbachian, F. Toarcian. Circles coloured by age on timeline to the left; numbers represent species richness.

4.6 ODONATA

There are 24 specimens identified as odonates (dragonflies and damselflies) from the Rhaetian, nine are identified to at least family level. The order is more abundant in the Hettangian, with 41 specimens known with 11 identified to at least family level. There are also 19 from the Upper Sinemurian and six from the Lower Sinemurian. All of the described specimens are from the suborder Epiprocta (dragonflies). There is also another specimen which is from the closely related extinct order Protozygoptera, also in the superorder Odonatoptera, which are damselfly-like insects (Nel et al. 2012b).

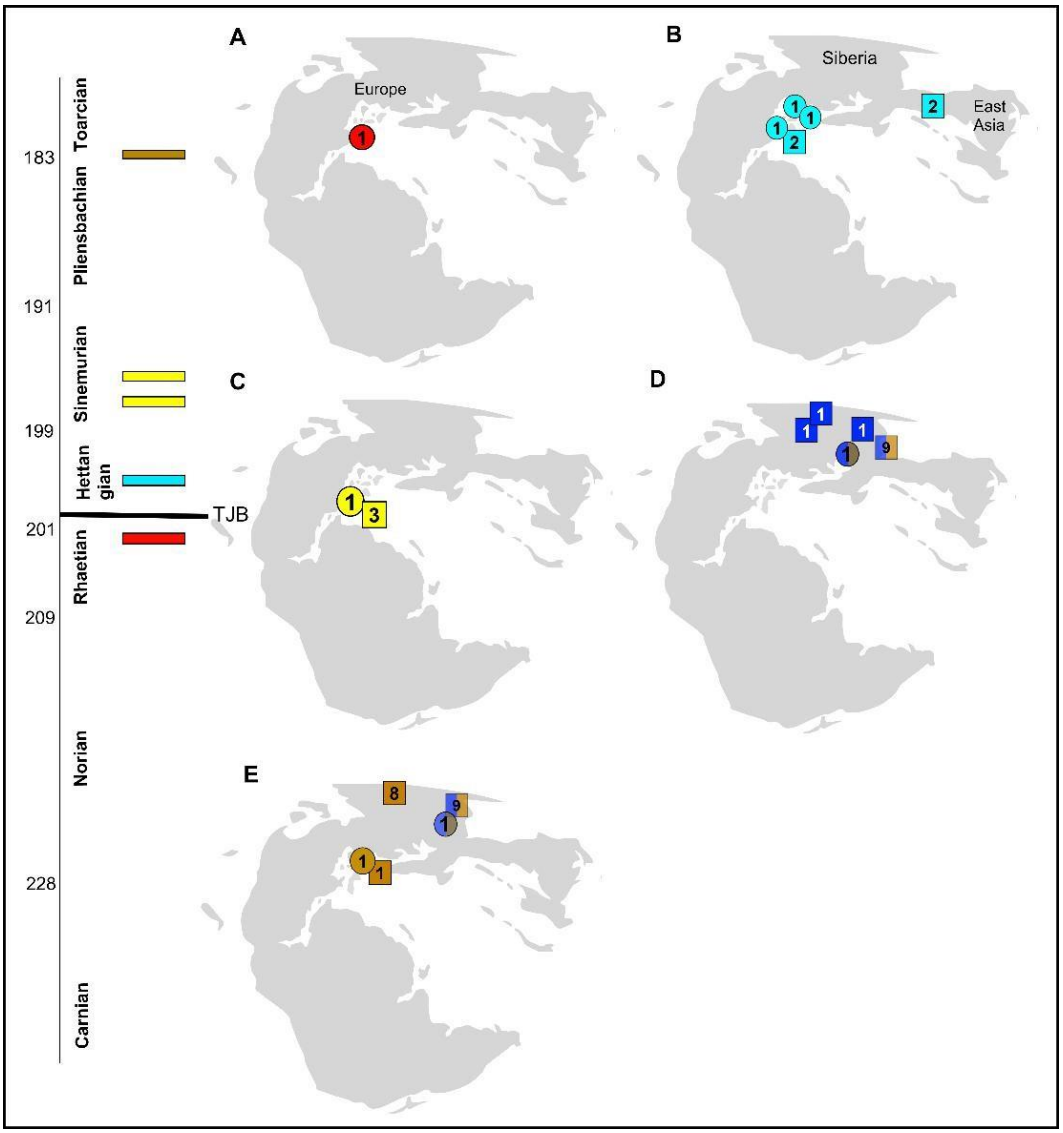

Figure 4.10. Global Late Triassic/Early Jurassic distribution of the odonate families Campterophlebiidae (squares) and Liassophlebiidae (circles). A. Rhaetian, B. Hettangian, C. Sinemurian, D. Pliensbachian, E. Toarcian. Shapes coloured by age on timeline to the left; numbers represent species richness.

There are five specimens identified as Liassophlebiidae from the Rhaetian (<1% of total abundance; 21% of odonates) in the genus *Liassophlebia*, two represent the species *L. withersi* and three are only

identified to genus level. There are another three specimens identified as two species which were previously assigned to this genus (*hopei* and *clavigaster*) but they are now considered *incertae sedis* at genus level (Kelly and Nel, 2018a). There are four specimens identified as Liassophlebiidae from the Hettangian (<1% of total Hettangian abundance; 10% of odonates), two of which are identifiable at species level, as *L. magnifica.* There are two genera and species known from the Upper Sinemurian, *L. pseudomagnifica* and *Rossiphlebia jacksoni*, both are only known from the Sinemurian and are not found in the older deposits. Liassophlebiidae and *Liassophlebia* are endemic to England in the Late Triassic but are more widespread in the Early Jurassic (Fig. 4.10) also being recorded in the Hettangian Gresten Formation of Germany, the Pliensbachian/Toarcian Sagul Formation of Kyrgyzstan, and the Toarcian Posidonia Shale Formation of Germany. There is also a specimen identified as *Liassophlebia* sp. from an unknown formation from France, estimated to be Hettangian in age.

Campterophlebiidae is not known from the English Rhaetian but there are five specimens from the Hettangian identified as '*Archithemis*' *liasina* and *Petrophlebia anglicana*. Both species are endemic to England, as is *Petrophlebia*, '*Archithemis*' is also recorded in the Toarcian Posidonia Formation of Germany, but '*A*' *liasina* is endemic to England. There are three specimens from the Upper Sinemurian, each identified as a different genus and species, *Dorsettia laeta, Hypsothemis fraseri*, and *Lateophlebia anglicanopsis*. Most species and genera are endemic to England, except for *Dorsettia* which is also known from the Hettangian/Sinemurian Badaowan Formation of China.

4.7 HEMIPTERA

There are 89 specimens identified as Hemiptera in the Rhaetian and 49 were identifiable to at least family level. There are 20 specimens from the Hettangian but only four of them are identified to at least family level. There are 56 specimens from the Upper Sinemurian, 42 of which are identifiable to at least family level and a further 76 from the Lower Sinemurian with 45 identified to at least family level. There are three relatively abundant families recorded in the Rhaetian, Dysmorphoptilidae with 16 specimens (2% of total abundance; 18% of hemipterans) all *Dysmorphoptila liasina*; Tettigarctidae with 14 specimens (1.5% of total abundance; 16% of hemipterans), 12 identified as '*Liassocicada*' *ignotus*; and Procercopidae with 10 specimens (1.5% of total abundance; 11% of hemipterans), nine are "Hem:Proc. sp. nov. 1", and one is "Hem:Proc. sp. nov. 2". The other families represented are Archegocimicidae (one specimen of *Britannicola senilis*), Hylicellidae (one specimen of *Homopterites anglicus*), Pachymeriidae (one specimen of *Pachymerus zucholdi*), Progoninumidae (one specimen of *Cicadocoris anglicus*), and two further Progonocimicidae specimens. In the Hettangian there is one *Protocoris indistinctus*, one *Lethonectes* sp. and one unidentified Tettigarctidae and one Archijassidae.

In the Upper Sinemurian, some of the families found in older deposits are also found: Belostomatidae (*Lethonectes naucoroides* and *Tarsabedus menkei*), Hylicellidae (*Mesocixiella*

fennahi), Pachymeriidae (*Neomeridium trifurcum*), and Tettigarctidae (*Shuraboprosbole rotruda*). Families first seen in the Sinemurian are: Corixidae (*Liassocorixa dorsetica*), Ochteridae (*Propreocoris maculatus*), and Pterocimicidae (*Pterocimex jacksoni*). The Lower Sinemurian is quite diverse for hemipterans, most of which are in the Coram collection from Monmouth Beach. There are eight families represented: Archegocimicidae, Archescytinidae, Belostomatidae, Dysmorphoptilidae, Fulgoridiidae, Pachymeridae, Pterocimicidae, and Tettigarctidae, but most are not identified any further.

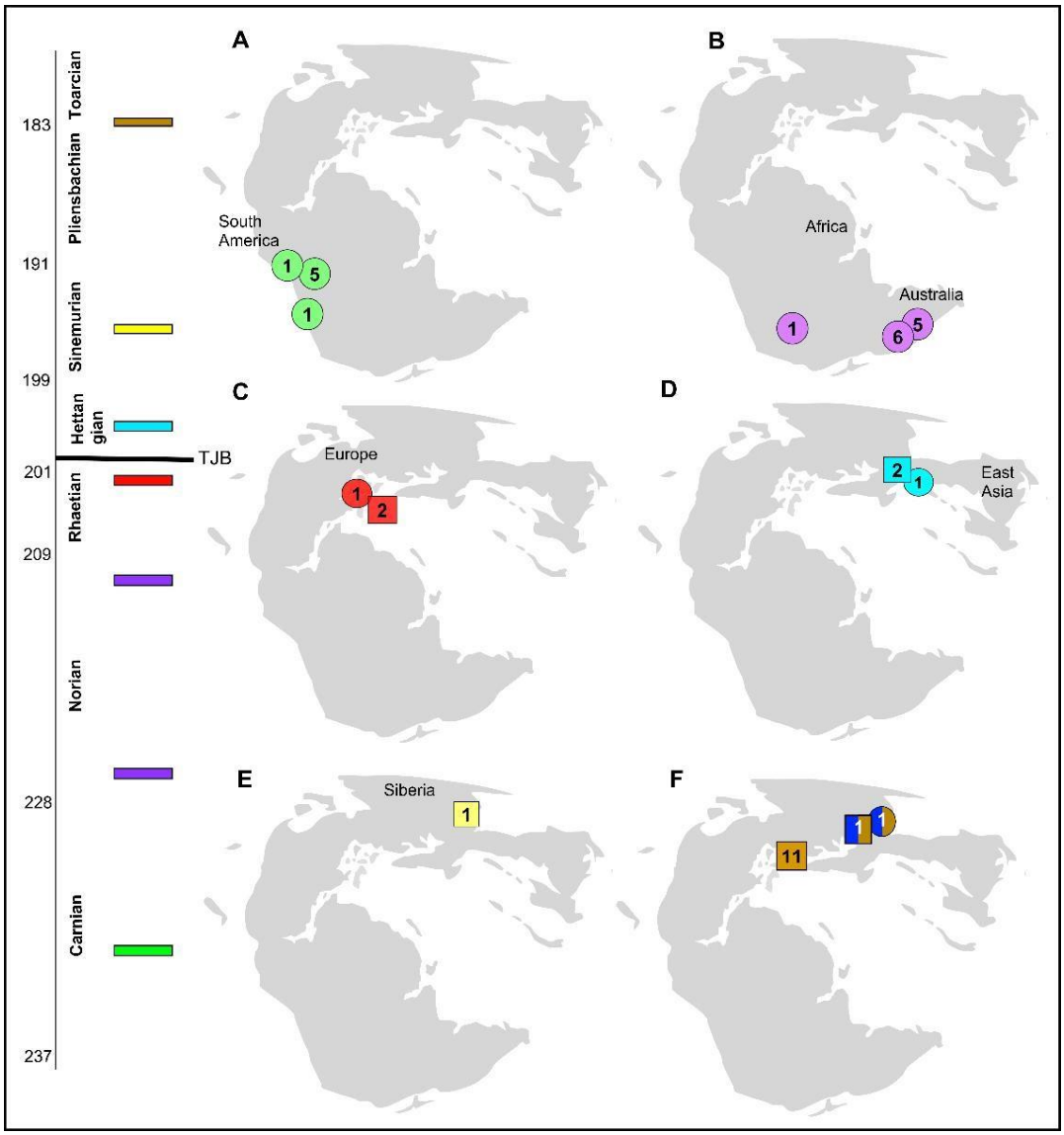

Figure 4.11. Global distribution of the Late Triassic/Early Jurassic bug families Dysmorphoptilidae (circles) and Procercopidae (squares). A. Carnian, B. Norian, C. Rhaetian, D. Hettangian, E. Sinemurian, F. Pliensbachian/Toarcian. Circles coloured by age on timeline to the left; numbers represent species richness.

All identified species are endemic to England in the Late Triassic. Dysmorphoptilidae is widespread in the Late Triassic of Gondwana (Fig. 4.11), also being recorded from the Carnian Los Rastros and Potrerillos formations of Argentina, the Carnian Santa Juana Formation of Chile, the

Norian Blackstone and Mount Crosby formations of Australia and the Carnian/Norian Molteno Formation of South Africa. It is very diverse in the Australian Triassic. *Dysmorphoptila* is endemic to England in the Triassic. Procercopidae and *Procercopis* are both endemic to England in the Triassic. Tettigarctidae is also recorded from the Carnian Hongweikeng and Huangshanjie, and Norian/ Rhaetian Sanqiutian formations of China, and the Carnian/Norian Molteno Formation of South Africa/Lesotho. '*Liassocicada*' is endemic to England in the Triassic, but the dataset suggests that Progonocimicidae is much more diverse outside of England, also being recorded in the Carnian Los Rastros Formation of Argentina and Madygen Formation of Kyrgyzstan, the Norian Blackstone and Mount Crosby formations of Australia, and the Norian/Rhaetian Tologoi Formation of Kazakhstan. Hylicellidae is more diverse outside England, with several more genera being recorded in the Blackstone and Mount Crosby formations of Australia. *Protocoris* is also record from the Hettangian Staffeleg Formation of Switzerland. These are also the only known occurrences of the family in the Early Jurassic. Belostomatidae is also recorded from the Hettangian Zagaje Formation of Poland and later in the English strata, from the Sinemurian Charmouth Mudstone Formation of the Dorset Coast.

4.8 Other orders

4.8.1 Dermaptera

There are 13 specimens identified as Dermaptera (earwigs) from the Rhaetian, all but one of which are identified to at least family level. There are four specimens from the Hettangian, with three identifiable to at least family level. There are four specimens known from the Upper Sinemurian, all of which are identified as *Brevicula gradus*, and a further three from the Lower Sinemurian, one of which is identified as *B. gradus* and another *B. maculata* which was also described for the present study (Kelly et al., 2018a). One species has complete dominance in the Rhaetian and Hettangian, *Phanerogramma heeri*, as all specimens identifiable to species level belong to this species. There is one specimen of *P. gouldsbroughi*, but it is not clear which formation the specimen was collected from and it is considered as either Rhaetian or Hettangian. Both species are endemic to England. The dataset suggests that *Phanerogramma* had a wide geographic range (Fig. 4.12), also being found in the Norian Blackstone Formation of Australia. There is another genus recorded in the English deposits, *Trivenoptera* from the Toarcian Beacon Limestone Formation (Kelly et al., 2018a). Both genera were previously endemic to England but are also possibly present in the Sinemurian Badaowan Formation of China (*Brevicula*) and the Toarcian Posidonia Formation of Germany (*Brevicula* and *Trivenoptera*) (personal observation of Chinese collections at NIGPAS and German collections held by Jörg Ansorge). There may also be some earwigs from the Argentinian Carnian (pers. comm. María Belén Lara, August 2018), but they require further verification.

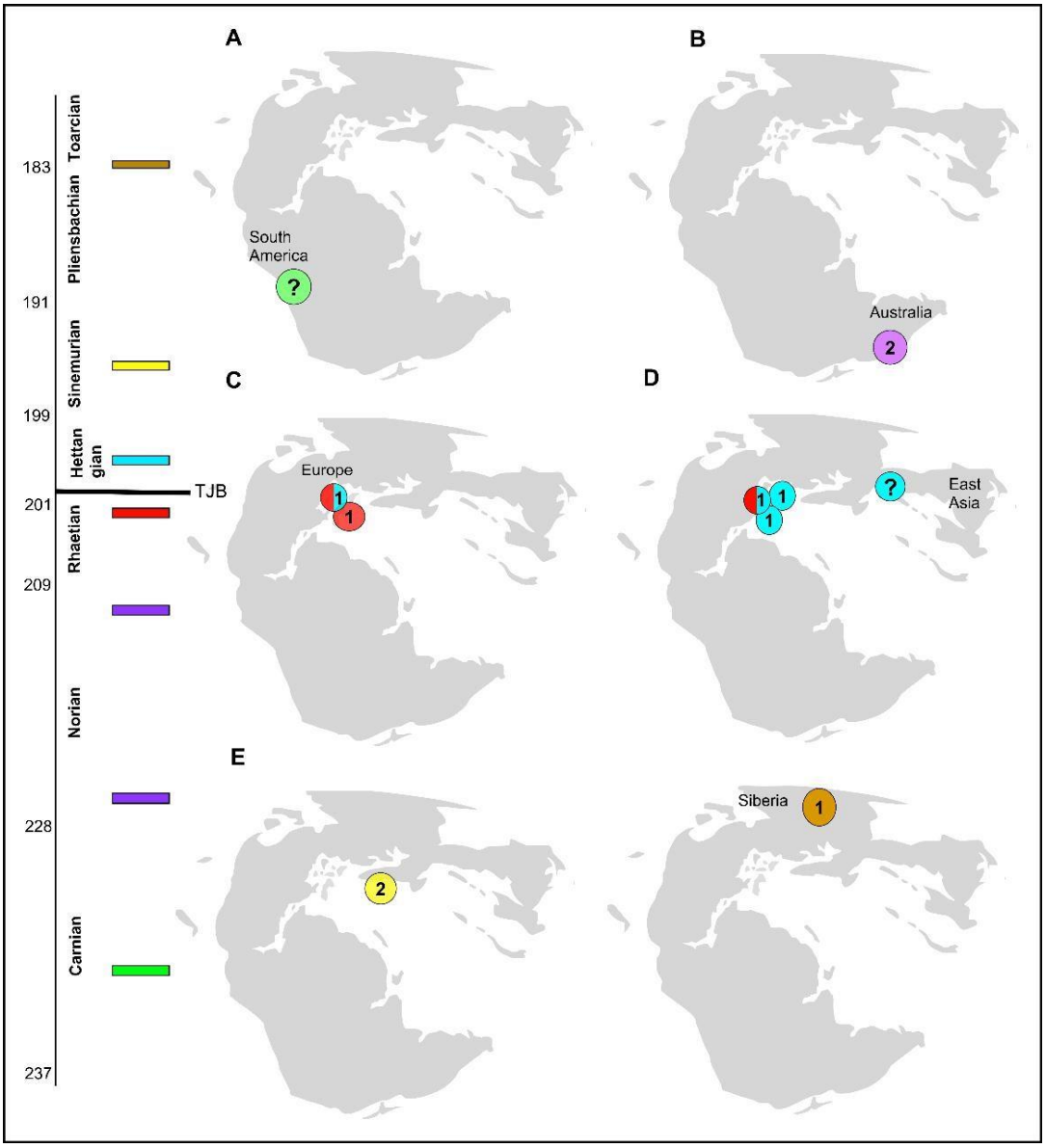

Figure 4.12. Global distribution of earwigs in the Late Triassic and Early Jurassic. A. Carnian, B. Norian, C. Rhaetian, D. Hettangian, E. Sinemurian, F. Toarcian. Circles coloured by age on timeline to the left; numbers represent species richness.

4.8.2 Trichoptera

There are 26 specimens identified as Trichoptera (caddisflies) from the English Rhaetian, 19 of which are identified to at least family level. There are only two specimens from the Hettangian. There are no trichopteran specimens from the Upper Sinemurian, but there are eight from the Lower Sinemurian, six from the Coram collection, one from the Carroll collection, and one which was in the Coram collection but was donated to NHMUK for description for the present study, it was described as the new genus and species *Austaulius haustrum* Kelly et al., 2018b. All but one of the Rhaetian/Hettangian specimens belongs to Necrotauliidae and all of those identifiable to species level are *Austaulius furcatus*, the other may belong to Philopotamidae: *Liadotaulius* but it is not entirely

clear. *Austaulius* is endemic to England. Necrotauliidae is also found in the Carnian Madygen Formation of Kyrgyzstan and the Toarcian Posidonia Formation of Germany. Similarly, this would be the only record of *Liadotaulius* in the Triassic, but Philopotamidae is also found in the Madygen Formation of Kyrgyzstan.

4.8.3 Neuroptera

There are six specimens identified as Neuroptera (lacewings) from the Rhaetian, all of which are identifiable to at least family level. There are 11 specimens identified from the Hettangian, three of which are identifiable to at least family level. There are nine lacewings from the Lower Sinemurian, all from the Coram and Carroll collections, four of which are identified to at least genus level. In the Rhaetian, there are two families known, Mesopolystoecotidae (*Megapolystoechus magnificus*) and Prohemerobiidae ("Neur:Proh. sp. nov. 2"). One other species (Prohemerobiidae: "Neur:Proh. sp. nov. 1") is also recorded in the Hettangian. The species is endemic to the Hettangian of England, but the genus is also found later in the English strata from the Toarcian Whitby Mudstone Formation, and from the same aged Posidonia Formation of Germany, in which the family is much more diverse. Prohemerobiidae is also recorded from the Toarcian Cheremkhovo Formation of Russia.

4.8.4 Blattodea

The Blattodea are also relatively underrepresented in the British Late Triassic/Early Jurassic with only five specimens collected from Rhaetian deposits, two from Hettangian deposits, four from the Lower Sinemurian, and eight from the Upper Sinemurian. The species present were not revised for the study as there was not the time but a project being led by andrew Ross is underway. There appear to be two species present in the Rhaetian, Caloblattinidae: *Rhiphidoblattina geikiei* known from two specimens and *Actinoblattula liasina* (family *incertae sedis*) known from one specimen. Only one species is known from the Hettangian, *Mesoblattina*? sp., in the family Mesoblattinidae. A further three species are represented in the Sinemurian, one *Nannoblattina* from the lower beds and two new genera from the Upper Sinemurian with a species each.

4.8.5 Diptera

There have been few Diptera (true flies) collected from these deposits but the order is relatively diverse given its low abundance. Five specimens from the Rhaetian identified as two species in two different families, Chironomidae (*Aenne triassica*) and Rhaetaniidae (*Rhaetania dianae*). There are none known from the English Hettangian, and there are no Hettangian aged species recorded in the dataset from anywhere in the world. There are then five specimens known from the Upper Sinemurian, identified as two different families to those from the Rhaetian, Oligophrynidae (*Oligophryne britannica*) and Ptychopteridae (*Eoptychoptera spectra*). The order is slightly more diverse in the

Lower Sinemurian, with 20 specimens from the Carroll and Coram collections identified as three species in two different families, Anisopodidae (*Megarhyphus amberae*) and Tanyderidae (*Nannotanyderus oliviae* and *N. krzeminskii*).

4.8.6 Lepidoptera, Raphidioptera, and Phasmatodea

Three orders are only known from the Sinemurian, namely, Lepidoptera, Raphidioptera, and Phasmatodea. Lepidoptera is known from one specimen representing Eolepidopterigidae: *Archaeolepis mane*, which was previously considered to be the oldest known fossil lepidopteran (Whalley, 1985) until fossil scales were uncovered from the Triassic of Germany (van Eldijk et al., 2018). Raphidioptera is known from three specimens, one represents Mesoraphidiidae: *Mesoraphidia confusa*, one represents Priscaenigmatidae: *Priscaenigma obtusa*, and the third is from the Carroll collection from the Pliensbachian of Dorset, the only known Pliensbachian insect from the UK, and probably represents a new species. Phasmatodea is known from one specimen representing Aerophasmatidae: *Durnovaria parallela* and is the only Sinemurian aged stick-insect in the dataset.

4.9 DISCUSSION

4.9.1 Comparison with other entomofaunas

The Swedish assemblage is the only other insect assemblage precisely aged to the lower Rhaetian, there are only seven species in the dataset, all of which are beetles. The assemblage is more diverse than this, but it has not been properly examined previously. Based on a survey of the collection at the SRMNH there are also several species representing Blattodea, Hemiptera, and Odonata which require description. It is still not a very abundant assemblage but does provide a contemporaneous but seemingly laterally variable assemblage compared to the English Rhaetian given the relative abundance of cockroaches in the Swedish fauna compared to the English fauna. Although there are no other upper Rhaetian horizons known there are several estimated as Rhaetian, although none of these are particularly abundant. Interestingly, the Çakrazboz Formation of Turkey, the unknown formation of Vietnam, the New Town and Mount Nicholas coal formations of Tasmania, and the Xiaoping and Xujiahe formations of China are all considered to be Rhaetian and have only produced cockroaches.

There are two other Hettangian entomofaunas known from Europe from the Polish Zagaje Formation, which is thought to be contemporaneous with the English fauna (Lower Hettangian), and the Swiss Staffeleg Formation, which is slightly younger (Middle Hettangian). There are five species described in the Polish assemblage, four of which are beetles and one is a water bug in the family Belostomatidae. The Swiss assemblage is abundant, with 800 specimens collected by Oswald Heer in the 19th century (Heer, 1865). There are 65 species in the dataset from this horizon, although we are currently revising them for an upcoming paper with Walter Etter at the Basel Museum of Natural History. Unlike the Lower Hettangian fauna from England, Coleoptera are dominant (71% of species

richness). This could suggest that beetle diversity was affected by environmental perturbation at the TJB leading to impoverishment in the Lower Hettangian which had recovered by the Middle Hettangian. There are issues with this though, including that the Swiss insects are found in a mudstone horizon, whereas the English Hettangian insects are from limestones, introducing potential facies related biases. There is also a small assemblage known from the Chinese Guanyintan Formation: Paijiachong Member aged as Hettangian, interestingly, as with the Rhaetian, although there are few cockroaches known from the English deposits, of the 13 species recorded from the Paijiachong Member, 12 of them are cockroaches. The Chinese Menkoushan Formation and the US Shuttle Meadow, Mount Toby, and Towaco formations may also provide Hettangian insects, but the ages of these formation cannot be resolved so highly, and they may also be Sinemurian.

There are two other formations estimated to the Lower Sinemurian, the Jinji and Badaowan formations of China. There are no other formations estimated to the Upper Sinemurian. Only one species is known from the Jinji Formation, a lacewing in the family Osmylidae. The Badaowan Formation is much more productive and there are hundreds of specimens held at NIGPAS awaiting description. There are 23 species in the dataset and interestingly the assemblage is dominated by scorpionflies (43% of described species richness). From a brief survey of the collections at NIGPAS, it is clear that this is not due to the specimens chosen for description. Scorpionflies are by far the most abundant in this fauna, more so than beetles or crickets.

The Dzhil Formation is estimated to the Sinemurian and is productive with 139 species in the dataset. Interestingly, this formation is particularly rich in flies (46 species, 33% of Dzhil species richness), whereas there are only 18 species of beetle. Martynova (1943) mentioned there being numerous flies and beetles collected from this formation, so again, there are not an abundance of flies simply because someone took an interest in them, but because they actually were rich in the taphocenosis. Several other Sinemurian-aged insects are known from the Mawson Formation of Antarctica, a dragonfly wing representing Campterophlebiidae which is also known from the Hettangian–Sinemurian of England, Sinemurian of China, and Sinemurian–Toarcian of Central Asia and Australia (Kelly and Nel, 2018b) and several which were recently brought to my attention including hemipterans and further odonates (pers. comm. Alycia Stigall, October 2018).

4.9.2 Palaeoecology of the British Triassic/Jurassic

Insects can be categorized based on a number of different attributes including feeding guild or morphological/physiological adaptations. A feeding guild represents a group of species which exploit the same resource and can be further split by diet breadth, which defines the specificity of a species for hosts/prey. There are three general categories for diet breadth which can apply to different guilds, monophagous, which means to feed on species in the same genus; oligophagous, which means to feed on several genera within the same family; and polyphagous, which means to feed on species from

more than one family (Price et al., 2011). As well as specificity for particular taxa, insects can further be categorised based on their specificity for particular parts of the host. They may be endophagous (feeding within the animal/plant) or exophagous (feeding without the animal/plant); herbivores may attach to the plant aboveground e.g. leaf chewers, stem/leaf sap suckers, and gall inducers; or belowground e.g. root chewers and root sap suckers; parasites may attach to certain body parts of the animal, or to certain life stages, or only to the parasites of certain life stages (Gullan and Cranston, 2010).

There have been several key morphological/physiological adaptations in the evolution of insects, namely: wings, wing folding, and complete metamorphosis (Nicholson et al., 2014). All of the insects known from the British deposits are winged and only one order (Odonata) does not possess wing folding, so only the latter adaptation is discussed further. Insects either undergo partial metamorphosis (Hemimetabola/Exopterygota), in which the juvenile insects, known as nymphs, look like small, wingless adults and usually occupy similar ecological niches to the adult; or complete metamorphosis (Holometabola/Endopterygota), in which there is a distinct juvenile stage, known as larvae, which occupy a different ecological niche to the adult (Gullan and Cranston, 2010) (Fig. 4.13). Larvae pass through a sessile pupation stage to reach maturity. Ecologically, the main advantage of holometabolism is that there is no lateral competition between the larvae and the adults.

Some ecological groups which are common today have little evidence in the pre-Cretaceous Mesozoic, indicating that they may not have radiated to the extent we see in today's ecosystems. There is evidence for most of these ecological behaviours, but it is usually based on ichnofossils and so can be difficult to assign to insect species based on body fossils. There are few obligate fungivorous insects, but insects do form close associations with fungi which may affect their survival. Wood eating insects ingest certain fungi to acquire them as internal symbionts that digest the cellulose in the wood that the insect eats, making the nutrients available to the insect host (Grünwald et al., 2010).

Figure 4.13 Left: Adult and nymph of hemimetabolous shield bugs (Hemiptera: Pentatomidae). Modified from Kelly (2016, fig. 6); Right: adults, larva, and pupal cases of holometabolous puss moths (Lepidoptera: Notodontidae), modified from Kelly (2014a).

Eusociality may not have been as widespread but there is some evidence of eusociality. Termite mounds are recorded from the Late Triassic of the US (Hasiotis and Dubiel, 1995) and the Early Jurassic of Zimbabwe (Bordy et al., 2004). Hymenopteran nests have been recorded from the Late Triassic of the US (Hasiotis et al., 1998), although other researchers have suggested that there is little evidence that these were hymenopteran nests and were probably made by wood boring beetles (Lucas et al., 2010). Subsociality, whereby adults show some form of maternal/paternal care towards the young but do not form complex social groups, was also probably present given that it is quite widespread in extant insects (e.g. some crickets, cockroaches, earwigs, bugs, thrips, and beetles). There are no known occurrences of insects associated with eggs in this way in the fossil record, but it is inferred with belostomatids from the Late Jurassic (Boucot and Poinar Jr, 2010).

Blood feeding (hematophagy) is thought to have been rare, although there are a few examples of potential Phthiraptera (lice) from the Late Triassic of India (Kumar and Kumar, 2001), although these have been questioned and may actually represent mites (see Nicholson et al., 2015, suppl.). Extant lice are obligate ectoparasites, feeding on the blood of vertebrates (Dick et al., 2009) Some insects are also known to feed on bone tissue (osteophagy), with evidence of insects chewing on dinosaur bones postmortem but pre-fossilisation as far back as the Late Triassic (Paes Neto et al., 2016), but mostly from the Late Jurassic (Britt et al., 2008). Extant bone chewers are mostly in the beetle family Dermestidae, which are known from the Norian of Australia but not from the TJB of Britain.

In the British TJB entomofauna several feeding guilds can be recognised, although we cannot categorise them to the same extent as extant insects. The largest group comprises the herbivores (phytophagous) which solely feed on living plant tissues, then the carnivores (creophagous) which solely feed on living animal tissues, omnivores (pantophagous) which feed on both plant and animal

tissues, and detritovores (saprophagous/necrophagous) which feed on dead or dying plant or animal tissues.

Bugs such as cicadas, froghoppers, planthoppers, and true bugs are sucking-type insects, which are mostly herbivorous in extant systems. They were probably mostly herbivorous in the Late Triassic as hematophagous forms had not evolved and only one bug with predatory extant relatives (Belostomatidae) is known. The earliest evidence of a hematophagous lineage of hemipterans is a crown group species of bedbugs (Cimicidae) from the Cretaceous (Engel, 2008). Hemiptera have a long piercing rostrum for feeding on internal plant fluids which is preserved in some Triassic specimens (Fig. 4.14). Most bugs were probably terrestrial, living in forested areas. Extant cicadas and planthoppers are largely forest dwelling with some associated with coniferous forests, e.g. some *Neotibicen* cicadas can be found singing in coniferous forests (Marshall and Hill, 2017) and several planthopper taxa are also found in coniferous forests, e.g. Achilidae (Arnett Jr, 2000). Some would probably have been associated with water in some way such as moss bugs (e.g., Progonocimicidae) and shore bugs similar to the extinct Archegocimicidae (Saldoidea), which generally live close to water or in moist habitats (Schaefer, 2009). Giant water bugs (Belostomatidae) are also known from as early as the Carnian (Criscione and Grimaldi, 2017) and are large active predators of freshwater systems preying on other invertebrates and small vertebrates. These are one of the few insects which exhibit paternal care, in which eggs can be laid on the male's back for protection until hatching (Phba et al., 2006).

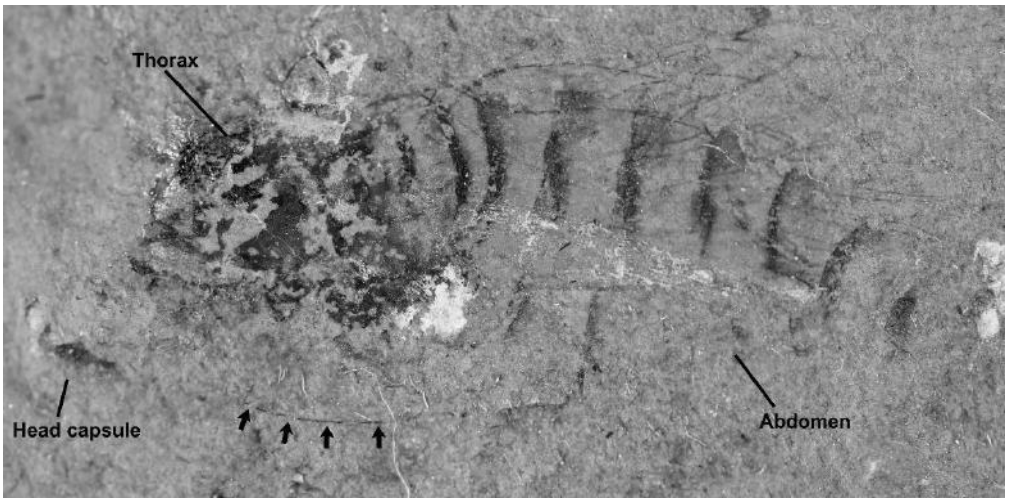

Figure 4.14 Triassic cicada preserving long rostrum used for piercing plant tissues (NHMUK 3538, '*Liassocicada*' *ignotus*, from Forthampton). Arrows indicate position of the rostrum.

Grasshoppers, stick insects, some beetle families (leaf beetles, click beetles, jewel beetles, ommatids), and early mandibulate moths represent chewing-type herbivores which predominantly feed on plant tissues externally. Grasshoppers and stick insects are hemimetabolous, but beetles are

holometabolous. Cupedid and ommatid beetles are today wood borers, which suggests woodland habitats (Coram, 2014), although the family today is much reduced. They were far more diverse in the Mesozoic and probably had a broader range of ecological habits. Other herbivores were lapping-type, such as some scorpionflies, fossils of which preserve a long, flexible proboscis used for feeding on external plant fluids (Pseudopolycentropodidae) (Shih et al., 2011). Also, several families of flies such as crane flies and wood gnats which can be quite diverse but are generally phytophagous.

Angiosperms had not evolved by the Triassic/Jurassic and so the vegetation of the time comprised gymnosperms such as tree and ground ferns, conifers, horsetails, clubmosses, spike mosses, and liverworts (see Chapter 1). The majority of extant insects feed on angiosperms, but there is a quite diverse assemblage of insects that feed on gymnosperms including planthoppers, beetles, sawflies, and leaf-miner flies (Poinar Jr, 2014). Drozd et al. (2008) found that approximately 25% of forest-floor dwelling insects are closely associated with bryophytes. Behaviours generally associated with angiosperms in extant systems are evidenced in the fossil record for gymnosperms. Folivory, feeding on leaves, has a long history, with evidence of insect damage on gymnosperm leaves as early as the Carboniferous (Iannuzzi and Labandeira, 2008). Skeletonization is often seen in extant angiosperms and has also been recorded in fern leaves in the Late Triassic of China (Feng et al., 2014). Some lineages of micromoth feed exclusively on liverworts, even in extant ecosystems (Imada et al., 2011). There is evidence of gall-inducing behaviour in insects as early as the Permian and throughout the Triassic (McLoughlin, 2011) and into the Late Triassic (Ash, 1996). This suggests that most of the niches associated with angiosperms today may have originated with gymnosperms prior to the Cretaceous, but the extreme specialisation and close cospeciation seen with insect-angiosperm interactions is not evident with gymnosperms.

Omnivores are represented mostly by crickets, which are quite taxonomically diverse in the British TJB. They are chewing-type mandibulate insects (Fig. 4.15) which usually feed on vegetation but are also known to feed on other insects (Sharov, 1968; Hahn and Kunert, 2006). Most of the crickets present are similar to extant bush crickets (Tettigoniidae) or true crickets (Gryllidae) both of which are generally omnivorous (Masaki, 1996). They are hemimetabolous. There are also some non-biting midges (Diptera: Chironomidae) which as larvae may inhabit a wide range of feeding guilds, but the adults tend not to eat, and caddisflies, which are also diverse in feeding style. Larvae may be predators, filter-feeders, or grazers and adults may feed on external plant fluids, or not at all (Gullan and Cranston, 2010). Some extant nonbiting midges and caddisflies are some of the only insects to live in marine habitats (Hashimoto, 1976; Riek, 1977).

Many of the insects associated with living plants (herbivores and omnivores) would have been pollinators of gymnosperms (Krassilov et al., 2007; Labandeira et al., 2007). Some cricket specimens (Haglidae) have been found in the Late Jurassic with pollen from the conifer *Classopollis*

(Cheirolepidiaceae) in their guts (Krassilov et al., 1997). Indicating that insect pollination was an important part of terrestrial ecosystems before angiosperms evolved.

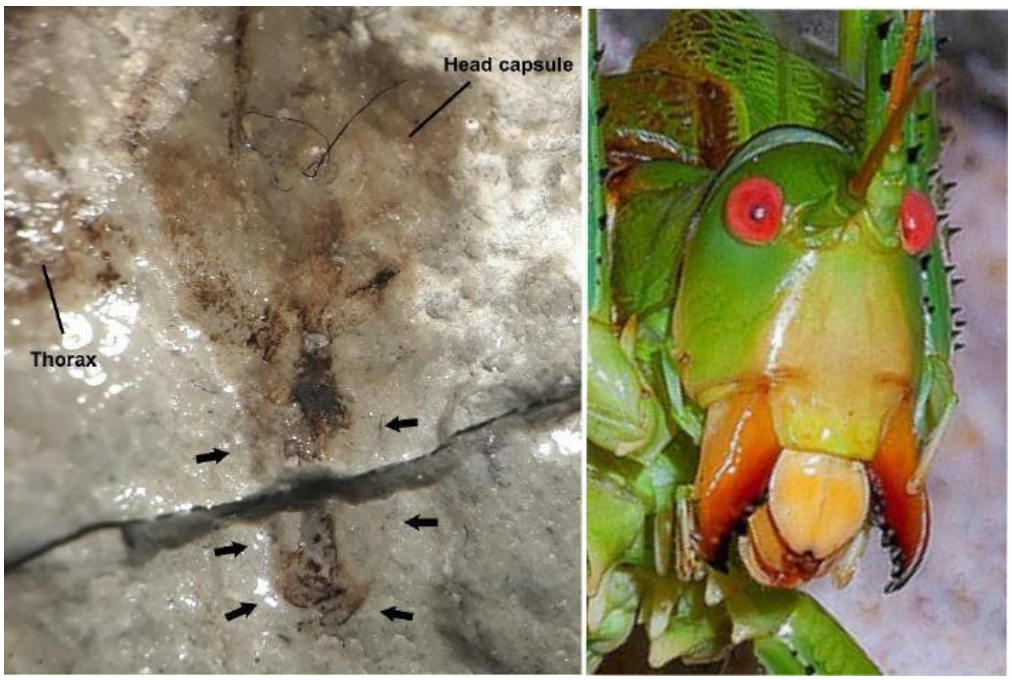

Figure 4.15 Ensiferan mouthparts from a Triassic bintoniellid (NHMUK I.11237 from Strensham) and an extant katydid (photo by Libutron). Arrows indicate fossilised mandibles.

Carnivores are represented by dragonflies, lacewings, snakeflies, hanging flies (Mecoptera: Bittacidae), and several families of predatory water beetles, namely, whirligig beetles (Gyrinidae), predaceous diving beetles (Dytiscidae), and coptoclavids (Coptoclavidae). There is a record of a ladybird beetle (Coccinellidae) assigned to an extant genus but this is unlikely. Some of these taxa represent terrestrial predators in both larval and adult stages (lacewings and snakeflies), which are relatively rare in the dataset. Hanging flies are terrestrial forest predators as adults but larvae are usually detritovores in forest floor litter. Dragonflies are terrestrial predators as adults but are usually closely associated with water, and their nymphs are active aquatic predators feeding on other invertebrates or small fish (Zwick, 2001). The predaceous beetles are all aquatic, the two extant families have active predatory larvae (Jäch and Balke, 2008).

Insects would also have been food for other animals (all carnivorous plants are angiosperms and there are no fungi that actively target insects). There are many examples of relatively small vertebrates from the Triassic/Jurassic which were probably insectivorous based on tooth morphology. Including rhynchocephalians such as *Clevosaurus* which were abundant in Britain in the Late Triassic (Keeble et al., 2018); crocodylomorphs, which were once much more diverse and included small, bipedal forms such as *Terrestrisuchus* from the Late Triassic of Britain (Crush, 1984) and Saltoposuchidae from the Late Triassic of Europe (Cloudsley-Thompson, 2005); pterosaurs such as *Peteinosaurus* from the Late Triassic of Europe (Cloudsley-Thompson, 2005); or other flying or gliding animals such as the

archosauromorph *Mecistotrachelos* (Fraser et al., 2007), or the squamate *Kuehneosaurus*, from the Late Triassic of Britain (Fraser and Walkden, 1983); small, basal mammals such as *Kuehneotherium* (Fraser et al., 1985); small avemetatarsalian pre-dinosaur archosaurs such as *Scleromochlus* and *Saltopus*, from the Late Triassic of Scotland (Benton and Walker, 2010); and small, therapod dinosaurs such as *Procompsognathus* known from the Late Triassic of Europe (Cloudsley-Thompson, 2005). There is also the potential for parasitic interactions with vertebrates but there is little evidence of hematophagy, and the earliest known fleas are from the Middle Jurassic (Leung, 2015). Other invertebrates would also have fed on insects, such as centipedes (Myriapoda: Chilopoda) or spiders (Arachnida: Araneae).

Detritovores include earwigs, cockroaches, some scorpionflies (Orthophlebiidae), and phantom crane flies (Ptychopteridae). Earwigs and cockroaches are hemimetabolous. They both show subsociality in extant species whereby the adults care for the eggs and/or nymphs (Rankin et al., 1996). The presence of cockroaches and earwigs, which are generally woodland floor, debris living scavengers (Gullan and Cranston, 2010), suggests some input into the depositional area from woodland habitats. Orthophlebiids are similar to the extant family Panorpidae which have elongated jaws terminating in chewing mouthparts used to feed mostly on dead or dying insects. Phantom crane flies are mostly terrestrial, with larvae living in moist swamp-like habitats and scavenging on decaying vegetation, whereas adults probably do not feed (andersson, 1997).

It is interesting that there are so few cockroaches in the British deposits when they are so prevalent in other similar aged deposits, often being the only insects recorded. This could lead to the assumption that there was some bias affecting the deposition of cockroaches. It cannot be a bias against leaf litter insects because the British deposits are some of the only deposits to preserve earwigs. anderson and anderson (1993) suggested that horsetail thickets from the Late Triassic of South Africa were associated with a lack of cockroaches compared to conifer forests, and higher relative proportions of beetles and orthopterans. This does seem to be consistent with the British insect assemblage except that the South African horsetail thickets were associated with very low diversity insect faunas, which is not the case for the British fauna. Perhaps it does suggest a greater role for the horsetail thickets and the riverine or riparian habitats of the British islands in the formation of the taphocenosis, with some forest insects making it into the system that transported insects to their deposition site but in fewer numbers. This would also explain the low numbers of entirely terrestrial insects such as lacewings and snakeflies, the latter of which is only known from the Sinemurian, and the complete lack of alderflies, dobsonflies, and fishflies (Megaloptera) or hymenopterans such as sawflies (Symphyta), which are known from other Late Triassic/Early Jurassic deposits.

Chapter 5. Taxonomic diversity trends across the Triassic/Jurassic boundary

5.1 Introduction

The Late Triassic saw several periods of major climate perturbations including a heightened period of humidity in the mid-Carnian associated with the rise of the dinosaurs and the origin of modern ecosystems of tetrapods (Benton et al., 2018). Similarly, with insects, there was a major loss of Palaeozoic forms during the Permian/Triassic mass extinction, and although Early–Middle Triassic insect assemblages are rare, there appears to have been a major shift through the Triassic, with more modern-like taxonomic structuring by the Late Triassic (Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005). Even though some of the more common orders had not radiated to the extent they currently enjoy (e.g. Lepidoptera and Hymenoptera), they had evolved by the Late Triassic.

During the Upper Triassic: Rhaetian, there is evidence for a period of massive perturbation in the Earth system; deposits of basalts around what would have been central Pangaea indicate large-scale eruptions of the Central Atlantic Magmatic Province (CAMP). From sedimentary deposits of this age, major shifts and declines in biodiversity and assemblage composition have been observed for marine (Mander et al., 2008) and terrestrial (van de Schootbrugge et al., 2009; Lindström, 2016) fauna and flora suggesting a major mass extinction event around the end of the Triassic leading to the transition to the Jurassic. Although there are ongoing discussions on the precise timeline of events surrounding the end-Triassic extinction (ETE; Lindström et al., 2017; Zaffani et al., 2018; Panfili et al., 2019), there is little doubt that this was a time of major change. However, previous studies have not reported a decline in insect family diversity at this time (Labandeira, 1994; Jarzembowski and Ross, 1996; Nicholson et al., 2015; Clapham et al., 2016). Given the evidence of rapidly changing climates and significant declines in plant diversity, it could be expected that insects would also have experienced a period of heightened extinction at this time, but perhaps analyses require examination of lower taxonomic levels to detect it (Ross et al., 2000; Nel and Prokop, 2009; Nicholson et al., 2015).

The global record of insect occurrence across the Triassic-Jurassic boundary (TJB) is quite extensive, with over 4000 fossils from England, at least 1000 from the rest of Europe, around 1000 from Australia, at least 2000 from the rest of Gondwana, probably 1000–2000 from East Asia and 10s of thousands from Central Asia (e.g. there are ~20,000 from the Kyrgyz Madygen Formation alone, Shcherbakov, 2008b), and therefore has the potential to be an extremely useful resource for investigating changes in the terrestrial realm at that time. Insects are key components of terrestrial ecosystems, and so it is worth attempting to document their macroevolutionary trends (Labandeira, 2005).

There are different ways to detect extinction signals in the fossil record. Global compilations gather together large amounts of data from often disparate sources and, through the calculation of different

metrics of diversity, establish long-term trends in diversity. Global compilations benefit from increased numbers of specimens and taxa, and although data usually cannot be split into high resolution time bins, in datasets such as that of the insects at the TJB, it is the only geographic scale to provide a complete stage-level series of insect occurrence. The UK data are abundant and diverse for certain key assemblages, but the lack of data from the Carnian, Norian, lower Rhaetian, middle– Upper Hettangian, and Pliensbachian hinders any analysis of long-term trends. This is somewhat resolved by scaling to a regional dataset that includes data from the UK and the surrounding area (Northwestern Tethys, NWT), but there are still major gaps in the data.

Problems for large-scale compilations of fossil data concern the integrity of datasets based on disparate sources and their resilience to new discoveries (Benton, 1999), as well as problems associated with low-resolution stratigraphic analyses. Some argue that time bins over 100 kyr may not be informative for fine-scale analyses of environmental change, and that diversity dynamics should be analysed in at least 1 Myr time bins (Renaudie and Lazarus, 2013). Unfortunately, given the difficulties with establishing a high-resolution timeline in the Late Triassic (see Chapter 1 and Kocsis et al., 2014), this resolution of analysis is not yet possible for the TJB. However, as well as improving stratigraphic resolution, it is also important to improve taxonomic resolution, and this has been done herein for the current data set.

The compiled correlation effect has also been noted, an artefact which artificially lumps extinctions from throughout a stage to the upper boundary, causing erroneously high estimates of extinction (Lucas and Tanner, 2018). This problem is somewhat resolved by improving the stratigraphic resolution of analyses where ever possible, and so dividing time bins and spreading extinctions back close to where they really occurred. High-resolution analysis of insect occurrence is hindered by the relatively sparse nature of productive insect-bearing horizons. Another method, advocated by Lucas and Tanner (2018), is the ‘best section’ approach; whereby, instead of compiling disparate global data, one particularly good section with abundant fossils in a series of high-resolution time bins through the event is analysed in detailed and then compared with other global sections. The UK series of insect limestones is quite extensive, with multiple horizons recorded from the lower Rhaetian–Lower Hettangian, and Lower–Upper Sinemurian. However, the vast majority of the Rhaetian and Hettangian fossils were collected from only one particularly productive horizon per stage (Rhaetian: Brodie’s Insect Limestone, with some additional fossils from the Landscape Marble, of the Lilstock Formation; Hettangian: the lower bed of the insect-bearing series in the Blue Lias Formation). The Dorset Coast series does offer a high-resolution account of insect occurrence in the Upper Sinemurian, and with further taxonomic work on recently discovered Lower Sinemurian material, it will provide data for the whole Sinemurian, but this is not very informative for examining the TJB without the same level of resolution from the older stages. There are no continuous sections of insect-bearing horizons across the TJB anywhere in the world, but the English data provides the closest to this. Rhaetian and Hettangian

horizons are found in a relatively small area of the English West Midlands and South-West regions, this being the only area in the world that is productive for upper Rhaetian and Lower Hettangian insects.

5.2 Materials and methods

A species-level dataset of insect occurrence was compiled from the Palaeobiology Database (PBDB). This is similar to the species-level data of Clapham et al. (2016), except it was restricted to the Triassic/Jurassic and certain sections were revised and updated based on the work carried out in this project. All UK specimens from public collections, and several private collections, were identified and revised where possible as per Chapters 2 and 3 and input into the dataset, including unpublished records of existing taxa and newly discovered taxa. Collections from Switzerland, Sweden, the US, and China were also examined, and any newly identified occurrences were also included in the dataset. The focus of the study is the TJB and insect diversity dynamics through the Late Triassic, but to put this in context the PBDB download also included all insect occurrences from the Early Triassic–Late Jurassic. The data were partitioned into three parts: UK, Northwestern Tethys (NWT), and global (GL). For the NWT series, the British data were bolstered with occurrences from the rest of Europe and eastern North America. During the Late Triassic, Western Europe largely comprised several archipelagos of small islands in relatively shallow epicontinental seas between North America and Siberia, with the British islands to the west. British ecology would have therefore been influenced by that of the American continent as much as the European islands.

There are no official substages for the Rhaetian, but previous studies have used unofficial substages defined by ammonoid zones (e.g. Kocsis et al., 2014) or palynomorph assemblages (Deenen et al., 2010) for the purpose of increasing stratigraphic resolution. The palynomorph-based 'substages' are defined based on the St. Audrie's Bay section in England, whereas the ammonoid zones defined by Kocsis et al. (2014) are difficult to correlate with British deposits, as much of the British Rhaetian is ammonoid-free. SAB1 of Deenan et al. (2010) mostly corresponds to the Westbury Formation and SAB2 and SAB3 correspond to the Lilstock Formation. Therefore, for the purposes of this study, the lower Rhaetian (LB 209.6, duration 4.1, mean age 207.45) is defined as the Westbury Formation, and the upper Rhaetian (LB 205.4, duration 4.1, mean age 203.25) as the Lilstock Formation.

The dataset comprises 4586 records of insect occurrences that are defined as the presence of a species/genus in a particular stratigraphic unit at a particular locality and represented by one row in the spreadsheet. Indeterminate taxa, e.g. "*Holcoptera* sp."/"Coptoclavidae gen." were removed if other records of the genus/family were reported, so as not to risk double counting. Although the UK occurrences can be precisely dated there is only one productive horizon in the Rhaetian and one in the Hettangian, so the data cannot be split into smaller time bins. Most of the NWT data can be dated to at

least substage, but only a few can be estimated to a higher resolution. The GL data can mostly be dated to stage level and around half (2218/4886 occurrences) can be dated to substage. For the main analysis, occurrences were not included if they did not fall within the analysed time unit (stage/substage) following previous studies (Kocsis et al., 2014; Clapham et al., 2016). The effect of the removal was negligible on the UK and NWT data as few formations were of uncertain age. The GL substage analysis, however, saw the removal of all Central Asian data, and with it most of the Carnian and almost all of the Pliensbachian data. To assess the impact of this on diversity dynamics, the GL substage analysis was run again; firstly, with occurrences included in each substage of their range (Benson et al., 2010), and secondly, randomly assigned to a substage within their range (Barbacka et al., 2017). This method is useful for assessing the effect these uncertain data have on diversity estimates. Ages were randomised 100 times and the mean calculated. There were some differences with the Carnian (Madygen Formation) and the Pliensbachian (Abasheva, Makarova, and Osinovka formations) estimates but there was only a small effect on the dynamics across the TJB, as almost all of the Rhaetian/Hettangian occurrences are precisely dated.

Data were imported into R Studio version 1.1.456 (R Core Team, 2018) for analysis using the package *divDyn* (Kocsis et al., 2018). I created a substage-level timeline based on Ogg et al. (2016) in the same format as the stage-level timeline provided in the package. The high number of single-occurrence taxa, especially at species level, limits the efficacy of many diversity metrics. Traditionally, range-based calculations (e.g. range-through, RT) have been used to estimate diversity and turnover rates based on first and last occurrences (Foote, 2000; Nicholson et al., 2015). RT calculates diversity based on all taxa that are present in, or have ranges that pass through, the interval and usually include single-interval taxa (Labandeira and Sepkoski, 1993), although some studies removed them (Sepkoski, 1997). These are useful metrics for converting compilations of first/last occurrences into a diversity curve but have been considered to be overly biased compared with metrics based on occurrence data (Alroy, 2008, 2010). Sampled-in-bin (SIB) is a measure of all taxa sampled in each time interval, without inferred ghost ranges. It does not suffer from most of the biases that range-based metrics do, but it is badly affected by sampling biases and is therefore usually subjected to sampling standardisation (Alroy, 2010).

Some studies have modelled diversity curves against sampling proxies, such as formation counts, in order to correct diversity metrics for sampling biases (Smith and McGowan, 2007; Nicholson et al., 2015). In defence of such models, some studies have found these corrections to outperform raw taxic counts for predicting diversity (Brocklehurst, 2015). However, arguments against these corrections are strong, and they have been rejected by some as mathematically unsound and based mostly on redundancy (Dunhill et al., 2013), concluding that they should not be used to correct fossil diversity data. Furthermore, formation counts are problematic as proxies of sampling bias, primarily owing to a

lack of independence from the data they are correcting. Benton et al. (2011) showed that in many cases formation counts will always correlate with counts of fossils, the so-called redundancy hypothesis. More comprehensive measures of sampling bias are preferred, such as specimen counts. We have abundance data for the UK, but not for NWT or GL.

Total specimen abundance for the UK was different in each substage—upper Rhaetian, 727; Lower Hettangian, 531; Lower Sinemurian, 356; Upper Sinemurian, 446—and it is unevenly distributed, with Rhaetian insects being collected from throughout the Severn Valley, whereas Hettangian insects are mostly from one locality in the north of the valley. However, the most abundant and speciose localities for Rhaetian insects are also in the north of the valley (Fig. 5.1). Even if we just consider the most abundant localities from each stage (Rhaetian: Strensham, 149 specimens, 29 species; Hettangian: Binton, 430 specimens, 24 species) it still implies a 17% drop in species richness from the Rhaetian to the Hettangian, even though in this calculation the Hettangian abundance is almost three times higher than that of the Rhaetian. Similarly, with the Sinemurian, although there are fewer specimens in both substages than the Hettangian, the species and genus richness are higher.

Although the revisions carried out for this project have much improved the record of insects in the UK, and to a lesser extent the NWT and GL series, there are still a large amount of single-interval, single-occurrence, and single-reference species, which makes SQS difficult, so we used classical rarefaction (CR) for the species data following Clapham et al. (2016). The genus data may suffer from similar problems but are more robust than the species data, so we analysed the genus series with both CR and SQS. SQS samples to a uniform frequency and can be corrected with a number of methods based on the proportion of either single-collection or single-reference taxa incorporated into Good's *U*. CR samples to a specific quota set during the calculation.

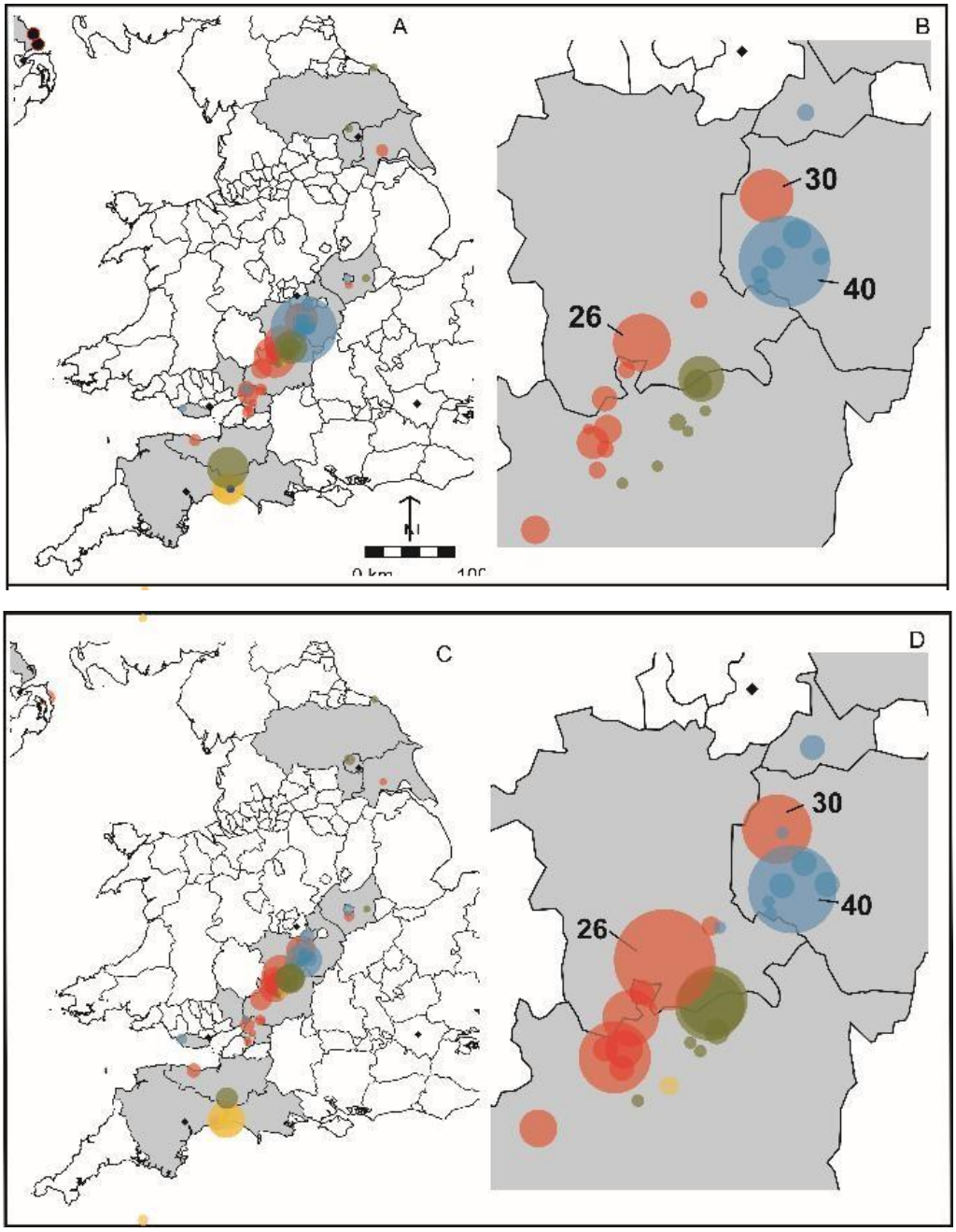

Figure 5.1. Map of UK insect diversity, A, B. total abundance; C, D. species richness. 26 = Strensham, 30 = Browns Wood, 40 = Binton. Colours indicate stratigraphic age as per previous chapters (red = Rhaetian; blue = Hettangian; yellow = Sinemurian, brown = Toarcian).

Herein, we present results based on the calculation of several metrics. They treat the data differently based on various aspects, such as stratigraphic patchiness and the abundance of single-collection/interval taxa, so using multiple metrics, certainly on the patchier UK and NWT datasets, allows an examination of the data from different angles. It also helps to facilitate comparisons with other studies that have used different metrics to estimate insect diversity.

1. Sampled-in-bin (SIB) is the main metric used as we have an occurrence-based dataset that allows us to estimate the taxa sampled in a bin, including many previously unpublished collections and all known occurrences of existing species alongside records of newly described taxa. Although range-based interpolation does not bias this metric, it is more affected by uneven sampling intensity; therefore, this series was also corrected using Alroy's three-timer measure, which, although suffering from increased estimation error, is considered to be the least biased estimate of diversity (Alroy, 2010; Kocsis et al., 2018).
2. Nicholson's minimum assumption (MIN) metric is also plotted. It is calculated as the sum of all first, last, and single occurrences in a stage/substage (Nicholson et al., 2015). The package *divDyn* returns these three counts in its standard metrics table, so these columns were summed and used to plot MIN. This is essentially RT including single-interval taxa minus the ghost ranges, acting as a subset of the SIB metric and is included for comparative purposes.
3. The range-through (RT) metric has problems with biases as discussed above, but it is an oft used method, that may be more suited to our species-level data given the almost ubiquity of single-interval species.

We also used the boundary crossers (BC) metric, which counts those taxa that crossed the lower boundary of the stage/substage (Alroy, 2010; Nicholson et al., 2015). All results returned a large increase in diversity from the Rhaetian to Hettangian. As the metric only counts those taxa that crossed the lower boundary of the time unit, it is of limited efficacy when all of the pre-Rhaetian Late Triassic intervals have zero data (UK) or very little data (NWT). BC is useful for tying diversity to a specific moment in time, i.e. the boundary, and so removes any problems with compilation effects. However, these are limited in datasets which do not have a spread of data through each time interval, where rather the vast majority of data are from one or two closely associated horizons.

5.3 Results

5.3.1 United Kingdom

There are 142 species and 95 genera recorded in the dataset from the Late Triassic/Early Jurassic of the UK (Appendix 6). Although the UK data are abundant, insects are concentrated in particular beds, with several stage and substages (Carnian, Norian, lower Rhaetian, middle/Upper Hettangian, Pliensbachian) having almost no data at all. This introduces difficulties when trying to establish long-term trends in diversity. The data do suggest a drop in SIB and RT diversity from the upper Rhaetian to the Lower Hettangian (Table 1) at both stage and substage levels for both genera (Fig. 5.2A, C) and species (Fig. 5.2B, D), increasing in the Sinemurian to similar levels as the Rhaetian. These data are from relatively well-sampled assemblages with recent taxonomic revisions and precisely dated stratigraphy.

Table 5.1. Insect diversity metrics partitioned for geographic scale (UK, NWT, GL), taxonomic level (species, genus), and stratigraphic level (stage, top; substage, bottom) analyses. MA is stage/substage midpoint. NWT = northwestern Tethys, GL – global, RT = range-through, BC = boundary crossers, SIB = sampled-in-bin, MIN = minimum assumption, MA = stage and substage midpoint, red band is the Rhaetian/upper Rhaetian, blue band is the Hettangian/Lower Hettangian.

MA	UK								NWT								GL							
	species				genus				species				genus				species				genus			
	RT	BC	SIB	MIN	RT	BC	SIB	MIN	RT	BC	SIB	MIN	RT	BC	SIB	MIN	RT	BC	SIB	MIN	RT	BC	SIB	MIN
232.5	NA	NA	NA	NA	NA	NA	NA	NA	28.0	2.0	27.0	27.0	32.0	8.0	27.0	27.0	578.0	4.0	574.0	576.0	352.0	41.0	336.0	325
218.25	NA	NA	NA	NA	NA	NA	NA	NA	34.0	1.0	33.0	33.0	34.0	9.0	26.0	25.0	262.0	5.0	261.0	283.0	192.0	56.0	159.0	165
204.9	78.0	NA	78.0	78.0	58.0	NA	58.0	58.0	100.0	2.0	98.0	98.0	82.0	13.0	76.0	72.0	111.0	4.0	107.0	107.0	120.0	50.0	84.0	74
200.3	38.0	16.0	38.0	29.0	34.0	18.0	33.0	19.0	71.0	22.0	70.0	60.0	75.0	39.0	60.0	43.0	86.0	24.0	84.0	74.0	113.0	74.0	68.0	46
195.05	79.0	15.0	76.0	75.0	63.0	20.0	60.0	57.0	81.0	17.0	77.0	76.0	81.0	41.0	61.0	52.0	262.0	19.0	258.0	256.0	211.0	82.0	168.0	147
186.75	4.0	4.0	NA	0.0	7.0	7.0	NA	0.0	7.0	7.0	NA	0.0	34.0	34.0	NA	0.0	70.0	12.0	58.0	63.0	122.0	92.0	44.0	33
178.4	20.0	4.0	20.0	20.0	17.0	7.0	17.0	17.0	510.0	7.0	510.0	510.0	296.0	34.0	292.0	288.0	613.0	31.0	600.0	600.0	391.0	108.0	348.0	321
236.25	NA	NA	NA	NA	NA	NA	NA	NA	11.0	1.0	10.0	10.0	14.0	5.0	10.0	10.0	60.0	1.0	59.0	59.0	47.0	14.0	37.0	36
234.5	NA	NA	NA	NA	NA	NA	NA	NA	2.0	1.0	1.0	1.0	8.0	7.0	1.0	1.0	20.0	1.0	19.0	19.0	28.0	17.0	14.0	11
231	NA	NA	NA	NA	NA	NA	NA	NA	12.0	2.0	10.0	10.0	18.0	8.0	10.0	10.0	47.0	2.0	45.0	45.0	53.0	22.0	38.0	32
223	NA	NA	NA	NA	NA	NA	NA	NA	24.0	2.0	23.0	23.0	25.0	8.0	18.0	18.0	126.0	3.0	124.0	124.0	111.0	22.0	94.0	91
215.75	NA	NA	NA	NA	NA	NA	NA	NA	1.0	1.0	NA	0.0	9.0	9.0	NA	0.0	8.0	8.0	NA	0.0	35.0	35.0	NA	0
211.8	NA	NA	NA	NA	NA	NA	NA	NA	12.0	1.0	11.0	11.0	17.0	9.0	9.0	8.0	143.0	8.0	141.0	141.0	93.0	35.0	78.0	75
207.5	1.0	NA	1.0	1.0	1.0	NA	1.0	1.0	17.0	1.0	16.0	16.0	28.0	10.0	18.0	18.0	17.0	2.0	15.0	15.0	37.0	21.0	17.0	16
203.4	77.0	NA	77.0	77.0	57.0	NA	57.0	57.0	83.0	2.0	82.0	81.0	67.0	15.0	60.0	55.0	95.0	3.0	93.0	92.0	82.0	25.0	70.0	62
201	38.0	16.0	38.0	29.0	34.0	18.0	33.0	19.0	54.0	21.0	50.0	41.0	62.0	38.0	44.0	28.0	54.0	22.0	50.0	41.0	65.0	43.0	44.0	28
200.4	15.0	15.0	NA	0.0	20.0	20.0	NA	0.0	35.0	19.0	23.0	18.0	54.0	42.0	21.0	15.0	36.0	20.0	23.0	18.0	58.0	46.0	21.0	15
199.8	15.0	15.0	NA	0.0	20.0	20.0	NA	0.0	17.0	17.0	NA	0.0	41.0	41.0	NA	0.0	18.0	18.0	NA	0.0	45.0	45.0	NA	0
197.95	46.0	15.0	38.0	34.0	40.0	20.0	31.0	24.0	48.0	17.0	39.0	34.0	60.0	41.0	32.0	22.0	71.0	18.0	62.0	57.0	74.0	45.0	46.0	34
193.95	53.0	20.0	50.0	49.0	48.0	25.0	43.0	41.0	55.0	22.0	51.0	50.0	69.0	48.0	44.0	36.0	55.0	22.0	51.0	50.0	71.0	52.0	44.0	36
189.85	4.0	4.0	NA	0.0	7.0	7.0	NA	0.0	7.0	7.0	NA	0.0	34.0	34.0	NA	0.0	7.0	7.0	NA	0.0	36.0	36.0	NA	0
186	4.0	4.0	NA	0.0	7.0	7.0	NA	0.0	7.0	7.0	NA	0.0	34.0	34.0	NA	0.0	7.0	7.0	NA	0.0	36.0	36.0	NA	0
181	20.0	4.0	20.0	20.0	17.0	7.0	17.0	17.0	510.0	7.0	510.0	510.0	296.0	34.0	292.0	288.0	509.0	7.0	509.0	509.0	296.0	36.0	292.0	288

The lack of data from the Middle/Upper Hettangian introduces difficulties in establishing trends between the Lower Hettangian and Lower Sinemurian, but it appears that following a Hettangian decline, diversity rises again in the Lower Sinemurian to reach almost Rhaetian levels again by the Upper Sinemurian. This is more pronounced at stage level (Fig. 5.2A, B), but the substage level analysis shows a more gradual increase through the Sinemurian (Fig. 5.2C, D). The Lower Sinemurian material was described as much as possible in the present study, but finer taxonomic work will improve our understanding of the diversity at this time. The BC metric counts only the taxa that cross the lower boundary of the time bin and the Rhaetian/upper Rhaetian data points are effectively counting the few taxa from the Norian/lower Rhaetian. Although it was not informative for long-term dynamics, what it does provide is an estimate of the taxa that survived the TJB, i.e. were alive exactly at the boundary. This metric reported that 18 genera (31% of the Rhaetian genera) and 16 species (20% of the Rhaetian species) crossed the TJB, compared to the overall decline in diversity of 51% species and 43% genera.

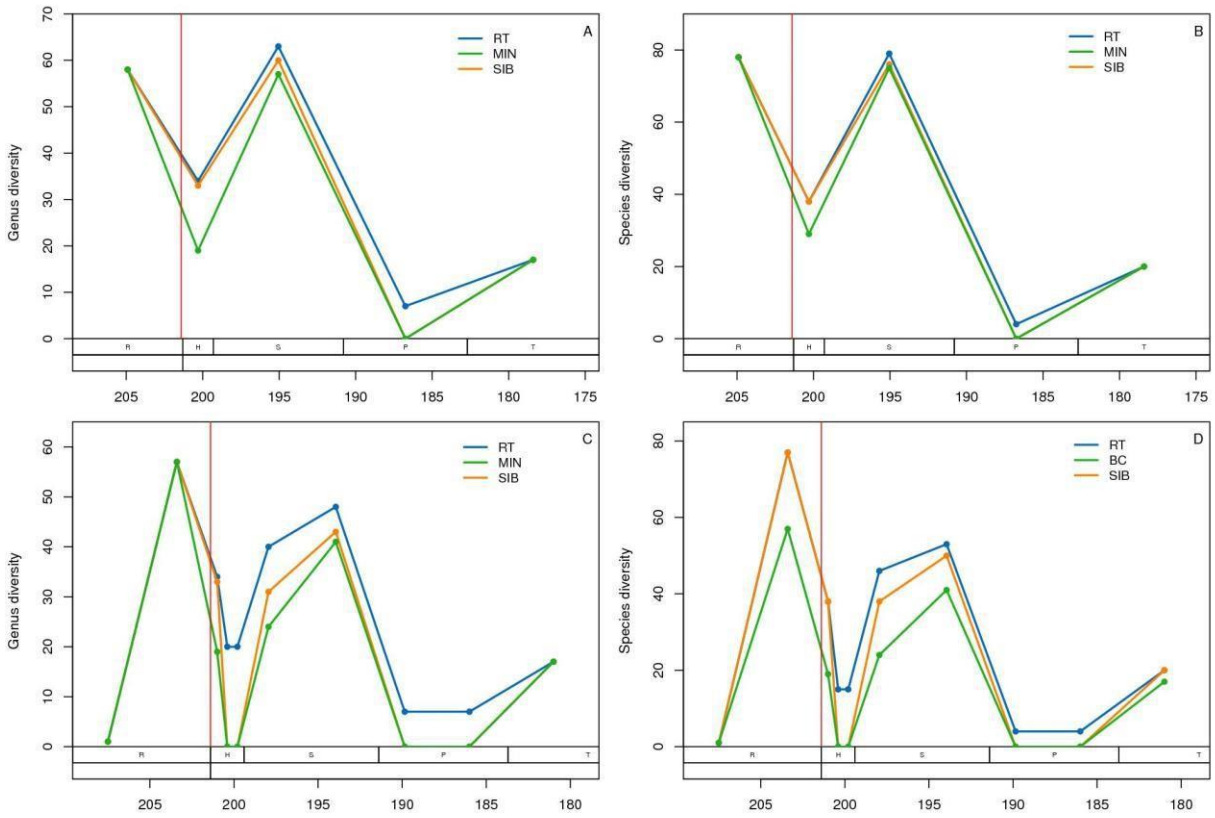

Figure 5.2. UK Late Triassic/Early Jurassic diversity curves. A. Stage level, genera; B. stage level, species; C. substage level, genera; D. substage level, species.

Diversity metrics were also calculated for the dataset pre-taxonomic revision. There were few differences in the broad diversity estimates based on pre- and post-taxonomic revision data with a decline of 53% species and 46% genera across the TJB. This means that the taxonomic revision carried out in the project had only a small effect on the broader estimates of diversity dynamics, but it did enhance our understanding of the finer scale changes in insect assemblages including species turnover, potential migrations, and shifts in dominance.

5.3.2 Northwestern Tethys diversity

The NWT dataset comprises 949 species and 533 genera. Both the SIB and RT diversity curves suggest an overall gradual increase in genus and species diversity throughout the Late Triassic (Fig. 5.3), with a slight dip in the Middle Carnian, a larger dip in the Middle Norian and then rising into the Rhaetian to decline more gradually into the Hettangian than the UK data. This provides an example of the compiled correlation effect (Lucas and Tanner, 2018), whereby diversity is pulled from throughout the Hettangian into a single data point, with all extinctions occurring only at the upper boundary of the stage. However, this is not evidence against an extinction event, but rather exemplifies the need for high-resolution stratigraphy. At substage level, this decline becomes much steeper, because the Middle Hettangian Swiss occurrences are separated from the Lower Hettangian occurrences. However, the Hettangian is a very short stage compared to the Rhaetian and Sinemurian, so this could be an artefact

of uneven time bins. This problem can be dealt with by analysing data in standard sized time bins (e.g. Clapham et al., 2016) or by lumping smaller substages together to have a stage/substage timeline (e.g. Kocsis et al., 2014). Trying to split the data any further would not work, as the vast majority of occurrences in each stage are from a single bed/horizon.

The decline is much more pronounced in the SIB data because this does not include the range extrapolations used in the RT metric. The RT metric includes taxa in all time bins between their first and last occurrences, so not all of the taxa reported by that metric were actually sampled in the Hettangian. In this sense, this is less useful for looking at changes in diversity because it does not pick out periods of local extinction, nor does it identify periods of increased rarity. Some taxa not reported in the Hettangian reappear in the Sinemurian. This does not necessarily mean that they went extinct, but it may imply that something caused them to either flee the local area or reduced their abundance and diversity to a point where they did not enter the fossil record.

When the SIB data are corrected to remove single- or double-interval taxa, only two data points are returned at stage level and so is not informative. These are revealed in the NWT data owing to the presence of Norian fossils, which are absent from the UK. Although no trends can be discerned, there a drop in generic diversity of 40% is implied from the Rhaetian to Hettangian at stage level. There is little difference between the RT and SIB metrics for the species data (Fig. 5.2B, D), indicating a high number of single-interval taxa and a lack of Lazarus taxa, as species are less likely to survive through three stages/substages than are genera. There is an overall drop in diversity across the TJB: at stage level, 29% species; 21% genera; at substage level: 35% species; 27% genera. The BC metric reports that 39 genera (51%) and 22 species (21%) crossed the TJB (Table 1).

As the regional dataset is from a wider geographic area and has a more complete stratigraphic succession, it can identify taxa that may not be recorded in the UK data. Some taxa were recorded as going extinct at the TJB as they were only found in the Lilstock Formation but scaling up to the NWT region shows that these taxa did not go completely extinct, e.g. *Bellingera* is also found in the Swiss Hettangian. It is unclear whether some of these taxa were present on the continent prior to the TJB owing to the dearth of productive insect-bearing Late Triassic deposits. Others, such as *Procercopis* that is also known from the Swedish lower Rhaetian and the German Toarcian, evidently survived the ETE on the continent but appears to have gone extinct locally in the UK. The genus was relatively abundant, with ten specimens and two species recorded from Brown's Wood but was not found in the Blue Lias or Charmouth Mudstone beds.

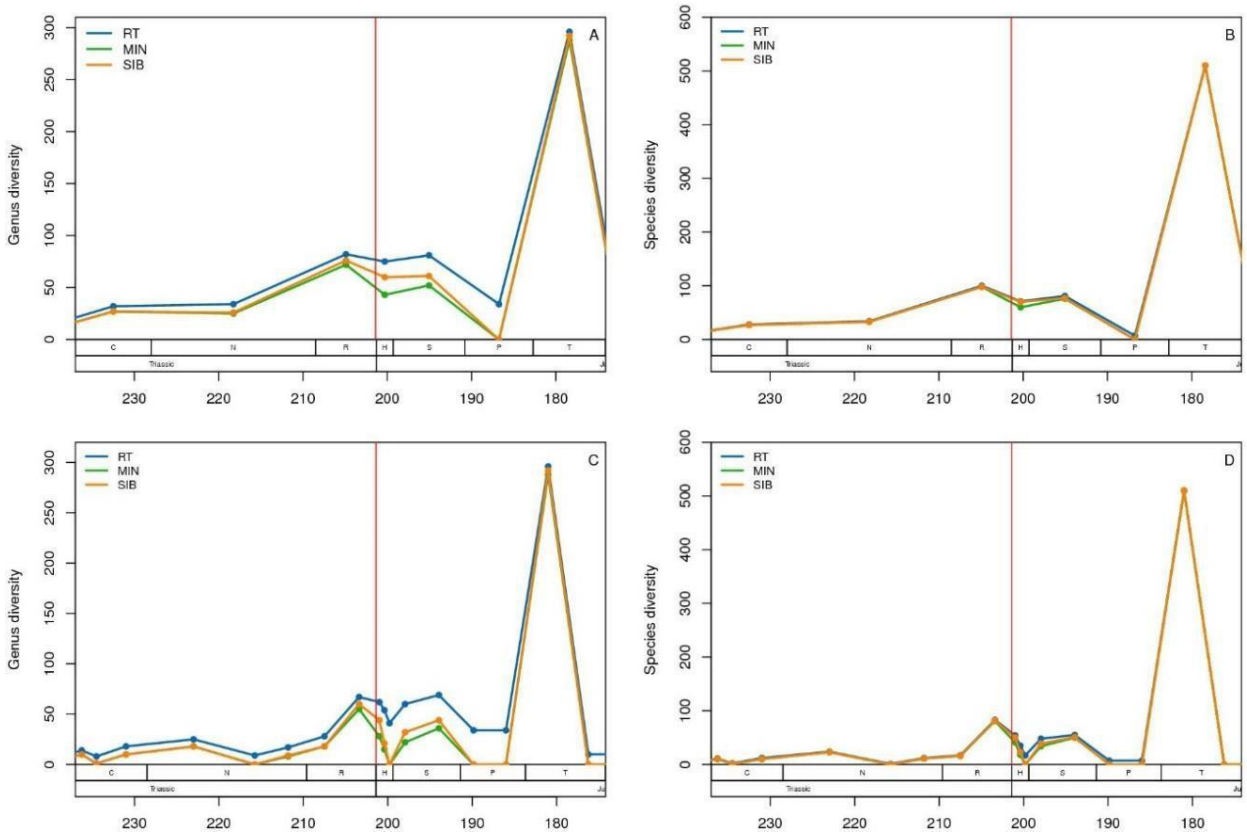

Figure 5.3. Northwestern Tethys Late Triassic/Early Jurassic diversity curves. A. Stage level, genera; B. stage level, species; C. substage level, genera; D. substage level, species.

5.3.3 Global

There are 2364 species and 1249 genera of insects recorded at the global level through the Late Triassic and Early Jurassic interval. The GL series is more complete stratigraphically than the UK or NWT series, notably filling in the gap in the Pliensbachian, providing much more data for the Carnian and Norian, and with abundant Sinemurian insects outside England. The overall trend observed in GL was the opposite to that observed in NWT (Fig. 5.4). There is a large increase in diversity from the Middle Triassic to the Carnian, leading into a long steady decline until the Hettangian. Most of the Carnian data are from the particularly productive Madygen Formation, producing a similar erroneous high to that in the Toarcian. This is evidently caused by a sampling bias, as there are 10s of thousands of insects collected from the Madygen Formation with a long history of revisionary work (discussed in Chapter 2).

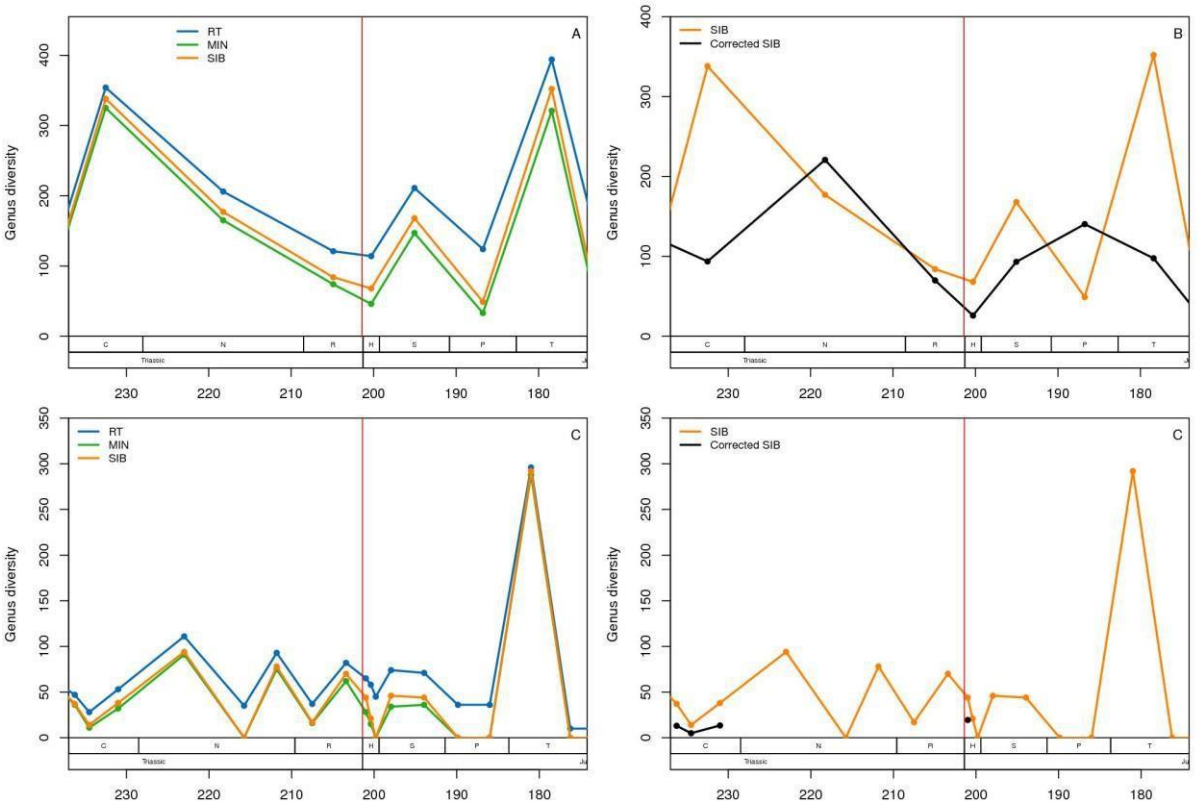

Figure 5.4. Global Late Triassic/Early Jurassic diversity curves. A. Stage level, genera; B. stage level, genera, three-timer corrected; C. substage level, genera; D. substage level, genera, three-timer corrected. Substage-level plots are with occurrences of unsure age removed.

At substage level, the Carnian high disappears, as does most of the trend observed in the stage-level data. Figure 5.4C, D shows the substage data with those formations of unsure age not included. The TJB decline in diversity is more pronounced. The curve is more jagged due to the lack of data in some substages (e.g. Middle Norian) and so the more pronounced drop in diversity from the Rhaetian to Hettangian could be considered to be a result of poor data, but there are abundant fossils from the Lower and Upper Norian, so it may be showing a reasonable account of the overall global diversity decline, gradually through the Norian and more sharply into the Hettangian. The species-level data cannot be corrected using methods based on taxa that cross boundaries, as many of the species are single-interval or even single-occurrence, but there are species that cross boundaries when there are the proper horizons to record them in the fossil record.

There are geographic and ecological fractures in the dataset between the Norian and Rhaetian, which exacerbate extinction estimates at that time. Most Rhaetian insects in the dataset are from England and probably represent some form of fluvial run-off from small tropical islands into a shallow brackish sea where they were deposited in fine grained limestones, whereas most of the Norian insects are from the Blackstone and Mount Crosby formations of Australia. At this time, Pangaea was still together, but it was still a considerable distance from England to Australia, crossing a range of biozones, as well as the equator. Insect genera have been reported from the Rhaetian of England and

the Norian of Australia (Kelly et al., 2018b), but it is unlikely that any species would have been shared between them.

There is a Norian insect-bearing horizon from the US which would have been geographically close to England during the Late Triassic, but this horizon represents a lacustrine habitat from the Lower Norian. Therefore, we would expect there to be few shared species based on ecological differences associated with their respective facies coupled with the time between them; the Norian was very long and there was at least 20 Myr between the Lower Norian and upper Rhaetian faunas. Again, however, this may not be such a problem at genus level, as there are genera reported from both the Rhaetian of England and the Norian of the US (Kelly et al., 2017). Insect genera were seemingly widespread geographically and stratigraphically, which improves the probability of their appearing in a patchy dataset if they are present, whereas the species-level data are less likely to because most countries only provide notable abundances of insects from few stages (e.g. Australia/US, Norian; Argentina, Carnian; Germany, Toarcian; Switzerland, Hettangian), increasing the probability of a species being reported as going extinct simply because no suitable insect-bearing horizon appears again within the stratigraphic, geographic, or ecological niche of the species following its initial report.

The data were corrected using Alroy's three-timer method, which provided a diversity curve for the genera at stage level (Fig. 5.4B), whereas running the corrections on the species-level data returned very little (Fig. 5.4D), similar to the UK and NWT data. In this diversity curve, both the Carnian and Toarcian highs are tempered, and the curve is not as volatile as in the previous curves. The curve dips into the Carnian from the Middle Triassic, rising again to a Norian high, before declining steadily through the Rhaetian, reaching its lowest point in the Hettangian, before rising again into the Pliensbachian when it starts to fall into the Toarcian. This is interesting as, even though there are issues with the dataset, it does seem to identify the major events of the interval. The dip in the Carnian could correspond with the Carnian Pluvial Event, recovering again in the Norian. The Toarcian Anoxic Event is also evident.

The long decline in diversity in the Late Triassic could suggest an extended period of species turnover from the Norian to Hettangian. It suggests a decline in diversity from the Ladinian to the Carnian, rising again into the Norian, consistent with reports of a Carnian-aged event of high taxic turnover and climate change (Carnian Pluvial Event; Benton et al., 2018). There is then a steady decline from the Norian into the Hettangian, with the Rhaetian sitting on the straight line between them, suggesting that the high extinction diversities reported in the UK and NWT data could be part of a longer decline in insect diversity from the Norian to the Hettangian. Indeed, one of the problems with the UK data was that it was not possible to determine any long-term trends or background levels of extinction because there was only one datapoint in the Late Triassic.

There were only a few formations that could not be dated to stage level, so almost all the data are included in the stage-level analyses. Conversely, there are major elements of the dataset omitted from

the substage-level analysis as they could not be precisely aged to a substage. This removes 10s of thousands of specimens and hundreds of taxa collected from the Central Asian and Russian formations (discussion of stratigraphy: Chapter 2, section 2.6.2). Therefore, these formations were included in the data by inputting them into each substage in their range (Benson et al., 2010). The Carnian and Toarcian highs return (Fig. 5.5A), and so the Late Triassic fall is pushed back to the Carnian again, representing the extremely high Madygen diversity. The mid-Carnian dip is still evident in the SIB and RT curves, before the diversity drops drastically into the Norian. The decline at the TJB is much more gradual, with the sharper drop pushed forward between the Lower and Upper Hettangian. The corrected curve agrees very closely with the SIB curve, except the mid-Carnian dip is more pronounced and the TJB drop is steeper, declining to the Lower Hettangian and then more rapidly dropping into the Upper Hettangian.

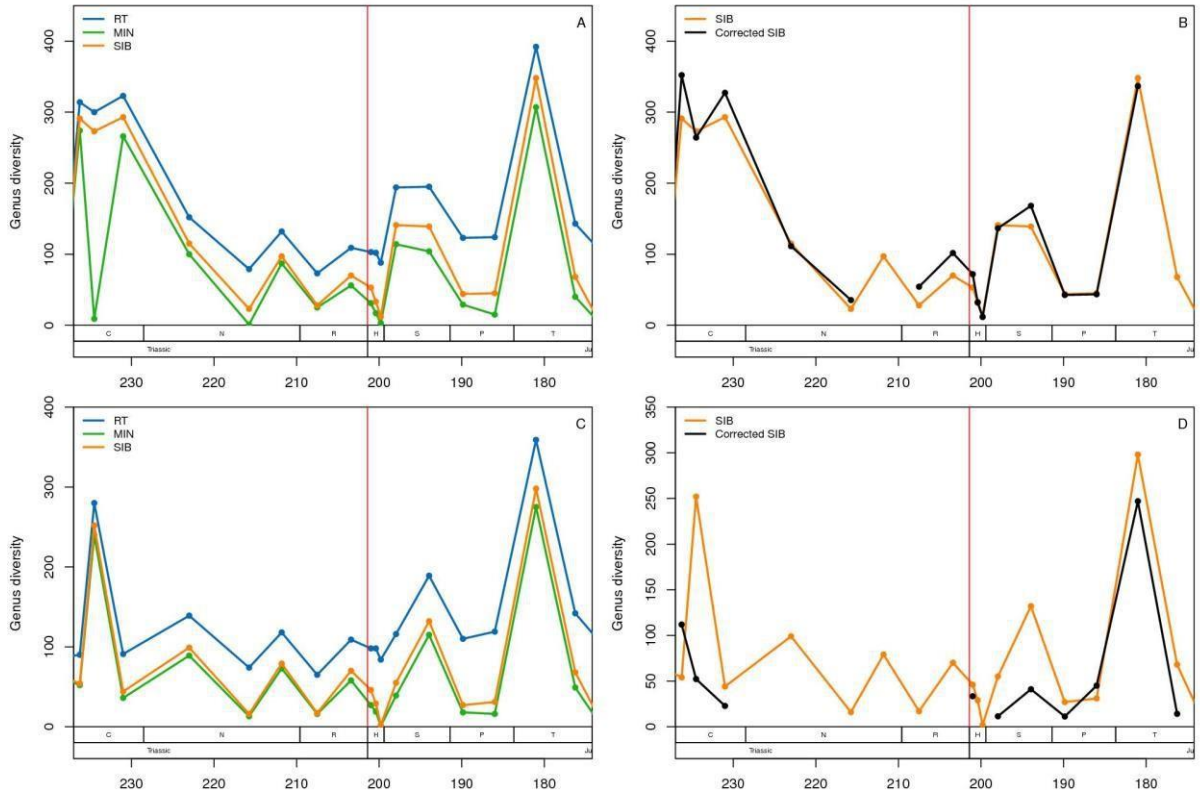

Figure 5.5. Global Late Triassic/Early Jurassic diversity curves. All at substage level, A,B with occurrences of unsure age included in all possible substages; C, D with these occurrences randomly assigned to a substage within their range. A, C diversity metrics; B, D three-timer corrected.

Confidence in this curve is not as high as with the stage-level analysis. The Late Triassic part, for which the SIB agrees almost exactly with its corrected curve, is probably caused by there being three substages in the Carnian and three in the Norian more than anything else, as the three-timer correction method counts those taxa that appear in three consecutive time bins. Therefore, the randomly assigned formation ages were also subject to the same diversity metrics (Fig. 5.5C).

The GL data seemed to provide promising results for establishing long-term trends in insect diversity through the interval of interest, at least when analysed at genus and stage level. When subjected to subsampling, the curve flattens out compared with the corrected SIB curve (Fig. 5.6A, B). The problem is that, subsampling is based on quotas and quorums that are determined by the nature of the data, and patchy datasets can lead to flattened curves arising from poorly fossiliferous time bins. There is, however, still the indication of a decline in diversity across the TJB in CR, subsampled at quotas of 50 and 70, and the SQS with quorums of 0.4 and 0.4 corrected with Good's *U* (very little difference). This was the highest quorum that resulted in a diversity curve; at 0.6 nothing was returned. The SQS 0.2 curve (and SQS 0.1, not shown) was the only curve to exhibit a slight rise in genus richness across the TJB. At substage-level, the diversity curve was almost zero for the three-timer corrected data when occurrences of unsure age were not included and was very broken with the randomly assigned ages (Fig. 5.5B, D). When included in all possible time bins, the substage data did return a corrected diversity curve and was subjected to CR and SQS subsampling (Fig. 5.6C, D). The curves are naturally patchier as some substages have no or very few data and most do not show the dynamics across the TJB, except for CR at 20 (Fig. 5.6C) and SQS at 0.6 (5.6D). The Good's *U* corrected curve does not show data at the TJB and is very patchy, but this is to be expected as Good's *U* is highly affected by single-interval taxa.

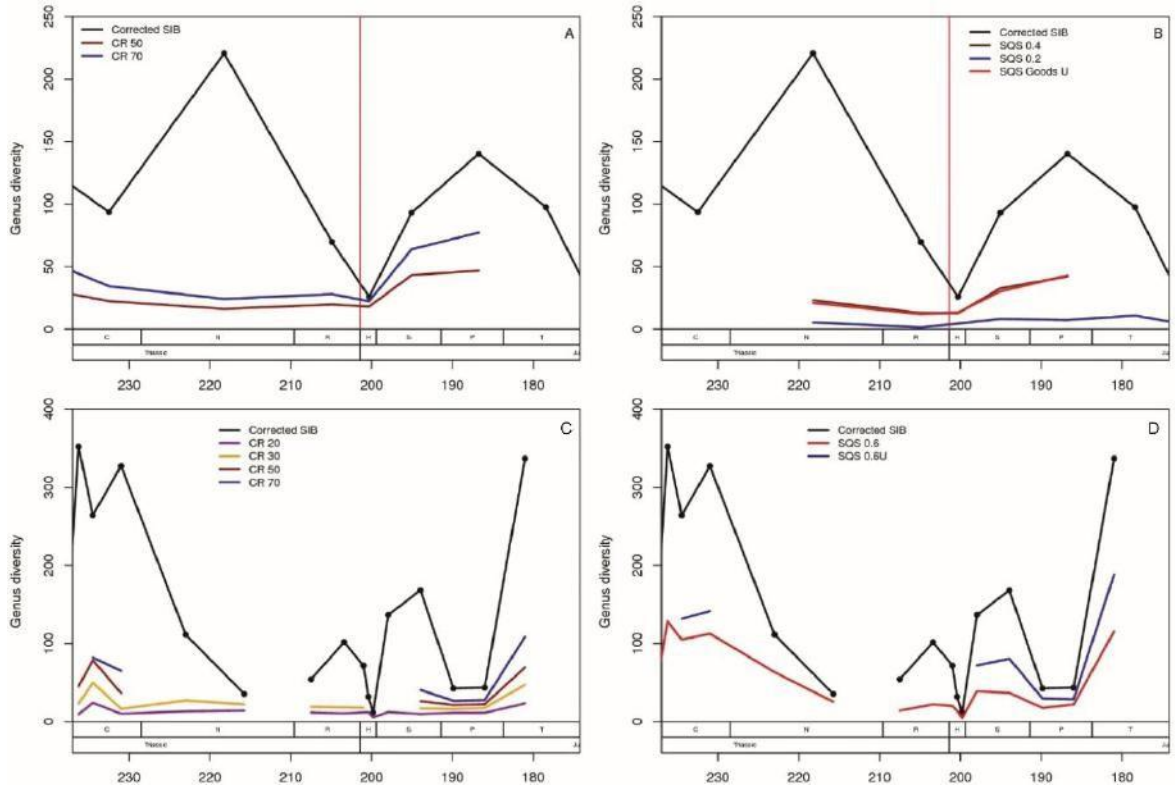

Figure 5.6. Global Late Triassic/Early Jurassic corrected diversity curves. A, B with occurrences of unsure age included in all possible substages; C, D with these occurrences randomly assigned to a substage within their range. A, C Classical rarefaction; B, D Shareholder quorum subsampling.

5.3.4 Extinction selectivity

To test the selectivity of the apparent drop in diversity across the TJB observed in the analyses in the previous sections, insect occurrence data were partitioned for broad ecological, evolutionary, and taxonomic groupings, according to the discussion in Chapter 4. Ecological groups were: herbivores, carnivores, omnivores, and detritovores; evolutionary groups were: Hemimetabola and Holometabola; and taxonomic orders were chosen based on their prevalence in the UK data: Coleoptera (beetles), Orthoptera (crickets/grasshoppers), Hemiptera (bugs); Odonata (dragonflies), and Mecoptera (scorpionflies).

It can be difficult to precisely assign fossils to ecological groups, especially based on fragmentary specimens that do not preserve indicative morphological characters, such as mouthparts for feeding group. It is usually possible, however, to assign insects to broad ecological groupings by relating fossils via taxonomy to related taxa with known ecologies. We can say, e.g. that the majority of extant caeliferans are herbivores or that the majority of extant odonates are carnivores, and thus can make general assumptions regarding the same groups in the past based on taxonomic similarity. Such assumptions made over millions of years can be tenuous but are bolstered by the similarity of these extinct insects with extant forms (all orders present in the British fauna are extant, as are some families, and a genus—*Omma*), and by the fossil record of other time intervals which preserve closely related taxa with morphological characters indicative of ecology. Other orders such as Coleoptera are so diverse that it would not be possible to precisely assign them to any ecological group based on isolated elytra, but certain families do have extensive fossil records.

The evolution of holometabolism is often considered to have conferred on these insects a robustness to extinctions compared to the hemimetabolous insects (e.g. Nicholson et al., 2012). As these are taxonomic groupings rather than ecological groupings, and as there are abundant data for each, we can partition our dataset to test whether this was true for the TJB at species and genus level. Holometabola include Coleoptera, Diptera, Odonata, Lepidoptera, Trichoptera, Neuroptera, Raphidioptera, and Mecoptera. Hemimetabola include Hemiptera, Orthoptera, Dermaptera, Blattodea, and Phasmatodea. Splitting the data in this way increases the prevalence of those groups that only occur in a single interval making statistical corrections less reliable. As the global genus-level data were found to be the most reliable in the previous analyses it was that dataset that was used in this analysis. The plots show the raw counts of occurrences of each group relative to one another to show the proportional change between groups rather than any absolute estimates of diversity for each group.

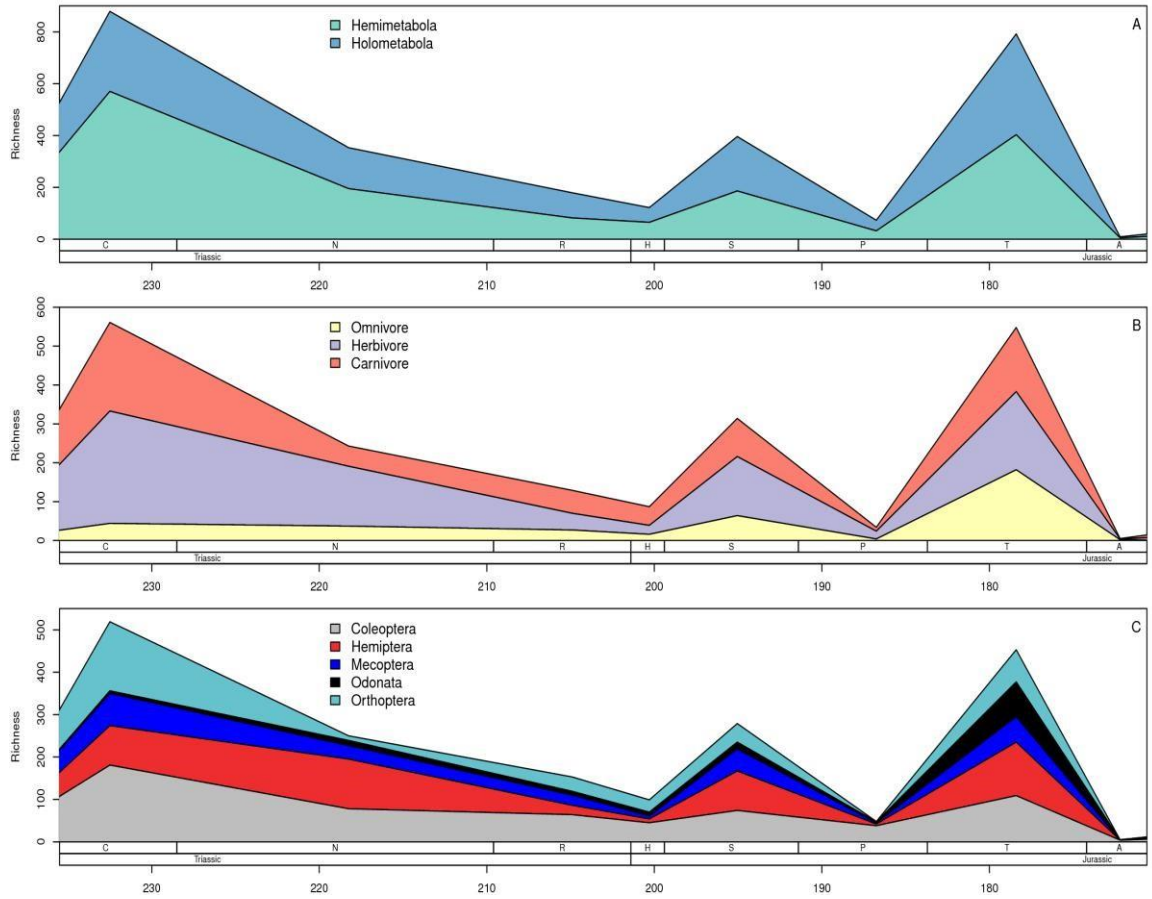

Figure 5.7. Extinction selectivity for Late Triassic/Early Jurassic insect genera at global level. A. Evolutionary selectivity, B. ecological selectivity, C. taxonomic (ordinal) selectivity.

In the Carnian, hemimetabolous insects were far more abundant than holometabolous insects (Fig. 5.7A), and although both groups apparently experienced a decline through the Late Triassic it is more pronounced for the Hemimetabola, with them having slightly less occurrences in the Rhaetian than Holometabola, but then the Holometabola have a greater decline across the TJB become less diverse than the Hemimetabola by the Hettangian. This probably represents the shift in dominance between coleopterans (Holometabola) and orthopterans (Hemimetabola) noted in Chapter 4 from the UK data. At stage level there are other sources of data from the Rhaetian and Hettangian outside of England, so it is interesting to see this trend appear in the GL data as well. At GL level, the orthopterans do not become more dominant than the coleopterans (Fig. 5.7C, teal and grey, respectively) but there is a dip in beetles across the TJB accompanied with a slightly less pronounced decline of orthopterans. Interestingly, the other largest hemimetabolous group are the hemipterans, and although the hemimetabolans seemingly fared better than the holometabolans across the TJB, this is certainly not true for the hemipterans (Fig. 5.7C, red). They exhibited dominance in the Norian before rapidly declining across the TJB, recovering again after the Hettangian, to share dominance with the coleopterans in the Sinemurian, and become more dominant in the Toarcian.

Interestingly, the number of omnivore occurrences (including the orthopteran crickets, Fig. 5.7B, yellow) seemingly did not change much throughout the Late Triassic and into the Hettangian. However, they massively increased relative to the herbivores and carnivores, both of which were declining, coming close to similar levels of diversity in the uppermost Rhaetian after which they slightly declined into the Hettangian, but the herbivores took their dominant position again by the Sinemurian. A steady rate of omnivores (including detritovores) with decreasing herbivores and carnivores may be explained by the oft generalist nature of omnivores and the more restrictive specialist diets of many herbivores and predators. Also, in a period of increased death, it would be expected that those organisms that feed on decaying organic matter (detritovores and some omnivores) would benefit compared to those that feed solely on living tissues (herbivores and carnivores). The post-TJB curve suggests that omnivores recovered to a more dominant position than pre-TJB as they comprise a higher proportion of the Sinemurian and Toarcian data points compared with the Carnian and Norian when herbivores were clearly dominant.

The odonates are the only group that appear to have had a relatively stable status within the assemblage throughout the Late Triassic and Lower Lias (Fig. 5.7C, black), becoming much more relatively abundant in the Toarcian, the only time when they are richer than the mecopterans. There is a point in the Norian when the odonates are relatively diverse compared to the orthopterans, but this is due to a massive drop in orthopteran abundance rather than anything changing for the odonates. Interestingly there appears to be a shift between the orthopterans and hemipterans from the Carnian to the Norian; similarly, the coleopterans decline in the Norian compared to the hemipterans. Both the Carnian and Norian are well sampled in Gondwana, so unlike the Laurasian dataset at the TJB it is much less patchy, with a series of relatively abundant horizons crossing the Carnian/Norian boundary in South Africa and diverse Carnian and Norian assemblages from Argentina and Australia respectively (see Chapter 2, section 2.6 for discussion). These insects are relatively well worked on recently and there is an ongoing project to revise the taxonomy of the historical collections from South Africa (Olivier Béthoux, pers. comm., August 2015). Once these assemblages are better understood they may provide a key resource for testing the Carnian Pluvial Event in the terrestrial realm of Gondwana.

5.4 Discussion

Most data presented herein suggest that there was an extinction event for insects in the Late Triassic, but the precise parameters of the event are difficult to delineate. Although there is evidently a decline in diversity from the uppermost Triassic to the lowermost Jurassic, most of the Rhaetian occurrence data are from the Lilstock Formation and, therefore, upper Rhaetian. This places the datapoint after the onset of the ETE as per Lindström et al. (2017), or just before the onset of the ETE as per Hillebrandt et al. (2013). Our data suggest that, even if the onset of the ETE was in the lower

Rhaetian, the effects of this on extinction levels appears to have persisted throughout the Rhaetian and into the lowermost Hettangian. Further data from the lower Rhaetian are necessary to establish whether there was a continuous decline through the Rhaetian or whether there was a higher diversity in the lower Rhaetian, dropping dramatically in the upper Rhaetian.

There are benefits to working with higher taxonomic levels when compiling large scale datasets, e.g. the taxonomy is generally more stable and the taxa range far enough geographically and stratigraphically to mostly overcome patchiness. There are indeed issues with working with species-level data, but it is certainly important to consider lower taxonomic levels when investigating extinction events, certainly in taxa such as insects that can have incredibly speciose and diverse families.

5.4.1 Coleoptera

Holcoptera is known from the Norian to the Sinemurian, having crossed the TJB and surviving the extinction event. The genus was rare in the Late Triassic with only two specimens recorded from the Norian (*H. solitensis*) and a further 20 from the Rhaetian, whereas there are 172 recorded from the Hettangian/Sinemurian. *H. giebeli* and *H. schlotheimi* both crossed the TJB, whereas *H. pigmentatus* was only alive in the Rhaetian. *H. schlotheimi* was dominant in the English Rhaetian and in the English and US Hettangian with *H. giebeli* becoming much more dominant by the Sinemurian. *H. alisonae* is only known from the English Sinemurian when it was slightly more diverse than *H. schlotheimi*. Therefore, it seems that although *Holcoptera* crossed the TJB, several species probably went extinct in the Late Triassic and there was a shift in the relative abundance of species that was potentially laterally variable across populations.

There were evidently wide-ranging populations of beetle species at the time that may have had complicated migration histories. *H. solitensis* was alive in the US Norian, but *H. schlotheimi* and *H. giebeli* are not recorded in the US until the Early Jurassic. There are a few possible scenarios. *H. solitensis* is the oldest species known from this genus, suggesting that *Holcoptera* originated in the Late Triassic of the US. *H. schlotheimi* and *H. giebeli* could then have also evolved in the US and migrated to England, but there are no Rhaetian-aged insect-bearing deposits in the US to record them, or earlier species could have migrated to England where *H. schlotheimi* and *H. giebeli* evolved and then migrated back into the US.

There is also some evidence for migration of other species after the event, e.g. *Bellingera ovalis* is recorded in the English Rhaetian but not the English Hettangian, but it is recorded in the Swiss Hettangian indicating that it could have migrated or gone extinct locally in England but survived in Central Europe. It is difficult to assess migration or local extinctions as other countries tend to produce insects from either the Late Triassic or Early Jurassic, rarely both. *Bellingera ovalis* may have been alive prior to the TJB in Switzerland but there are no deposits to record it. These records suggest that

there was migration of insect species between England and North America and England and continental Europe during the Late Triassic/Early Jurassic.

5.4.2 Orthoptera

There are two genera of grasshoppers recorded in the family Locustopseidae. *Locustopsis* crossed the TJB ranging to the Sinemurian, as did *Mesolocustopsis*, which was alive until the Cretaceous (Sukacheva and Jarzembowski, 2001). There are five species identified in *Locustopsis*, one (*L. cubitalis*) is unknown after the TJB, two (*L. lacoei* and *L. spectablis*) crossed the TJB going extinct in the Hettangian, whereas *L. ornatum* and *L. anglicana* are known only from the Sinemurian. *L. lacoei* and *L. spectablis* were rare before and after the TJB, so there is little difference in relative abundance. *Locustopsis* appears to have originated in the English Rhaetian but the family is known from the South African Permian (Riek, 1976). As with previously discussed taxa, *Locustopsis* seems to have had a much wider geographic range in the Early Jurassic as it is also known from the Kyrgyz Sinemurian, Tajik Pliensbachian, and German Toarcian suggesting possible eastwards migration following the TJB. This may, however, be an artefact of a patchy Late Triassic European dataset.

Haglopsis (Bintoniellidae) crossed the TJB, as did the two species identified in this genus, *H. parallela* and *H. brodiei* but there was a shift in relative abundance, with *H. parallela* slightly declining across the TJB, but *H. brodiei* increased in abundance surpassing *H. parallela*. However, *H. brodiei* is not recorded in the Sinemurian, whereas *H. parallela* is, suggesting that, even though there was a decline in the dominance of *H. parallela* from the upper Rhaetian to the Lower Hettangian, the species persisted into the Sinemurian, whereas *H. brodiei* was only abundant for a short time, flourishing in the Lower Hettangian. The earliest records of Bintoniellidae, and the only ones from outside of England, were from the Kyrgyz Carnian but all genera were endemic and not recorded at any other time, so they probably went extinct in the Late Triassic.

There are three species of *Archelcana* recorded. *A. liasina* crossed the TJB, increasing in abundance in the British Hettangian and occurring for the first time in Switzerland. The species persisted fairly consistently into the Sinemurian. *A. partitus* is known only from one specimen in the Rhaetian. *Archelcana* was rare in the Late Triassic but is also known from the German Norian. It was more widespread in the Early Jurassic as it is also known from the Toarcian of Kyrgyzstan, Russia, and Germany. It is not recorded in the Madygen Formation, suggesting that it was not present in Central Asia in the Carnian but rather seems to have originated in Europe and migrated eastwards during the Early Jurassic.

Protogryllus ranged from the Rhaetian to the Toarcian, but the species-level turnover was also more complex. of the four species identified, only *P. parallelus* crossed the TJB, but is not known after the Hettangian, *P. grandis* is unknown after the TJB and *P. magnus* appears to have originated

following the TJB ranging to the Toarcian. *P. acutipennis* is known only from the Toarcian. *P. magnus* and *P. acutipennis* are also recorded in the German Toarcian suggesting wider geographic ranges in the Early Jurassic. There are few productive Rhaetian, Hettangian, and no Sinemurian insect-bearing horizons from Germany, so it is difficult to say whether they were also present earlier or whether they migrated from England sometime after the TJB.

Haglidae has two genera, each with a single species, recorded in the Rhaetian (*Hagla* and "Orth:Hag. gen. nov.") which both survived into the Hettangian but are unknown in the Sinemurian. *Hagla gracilis*, and the whole family, dropped in abundance from the Rhaetian to the Hettangian, in contrast with other families, indicating a shift in relative diversity within Orthoptera. There was another genus (*Liassophylum*) which is first recorded after the TJB and is only known from the Hettangian, and one more (*Protohagla*) which is only known from Sinemurian deposits. Haglidae is very diverse in the Kyrgyz Carnian, ranging in Central/Northern Asia through to the Toarcian. It is also known from the Australian Norian, but there are no records of the family in the Late Triassic of Europe until the English Rhaetian. Given the diversity of the family in the Carnian and that it was present in the English Rhaetian we would expect to see records of the family in the Norian and Rhaetian of Europe. It could be the case that the family did not expand into Europe until the upper Rhaetian, or that the family was present throughout Europe in the Norian and Rhaetian but is not being picked up by the fossil record.

5.4.3 Mecoptera

For the scorpionflies, only *Orthophlebia* crossed the TJB and of the nine species recorded from the UK, only *O. liassica* is recorded from Triassic and Jurassic deposits. The other four species recorded from the Rhaetian are not known after the TJB and two appear in the Lower Hettangian. Seven other species were recorded in the Rhaetian from three other families (Bittacidae, Mesochoristidae, and Worcestobiidae) and two other species were recorded in the Hettangian in only one other family (Liassophilidae). The evidence suggests an almost complete species turnover from the Rhaetian to Hettangian (four out of five species) with an impoverished assemblage in the Hettangian (five Hettangian species, compared to 12 Rhaetian species).

The first occurrence of Orthophlebiidae (and *Orthophlebia*) was in the Kyrgyz Carnian and the family is also found in the Chinese Carnian. Then it is not recorded again in the Late Triassic until the English Rhaetian. In the Early Jurassic the genus appears to expand and radiate much further being recorded from the Chinese Hettangian, Kyrgyz Sinemurian, Tajik Pliensbachian, Russian Pliensbachian and Toarcian, German Toarcian, and Kazakh Early Jurassic. Although the Early Jurassic record is richer than the Late Triassic one the recording of family in the Chinese Carnian suggests that this family was already widespread by the Late Triassic.

5.4.4 Odonata

From the overall species richness estimations, there was a slight increase in damsel-dragonfly species richness from the Rhaetian to the Hettangian but none of the species recorded in the Rhaetian are also recorded in the Hettangian. *Liassophlebia* crossed the TJB in England but *Progonophlebia* is unknown thereafter. It is unlikely that that there was a complete turnover of species from the Rhaetian to Hettangian, but these results may suggest a high level of perturbation to the ecosystem or shifting dominance at the genus or species level. There is further evidence from the dragonflies for an eastward migration in the Early Jurassic. Liassophlebiidae (and *Liassophlebia*) apparently originated in the Rhaetian, when it was endemic to England. *Liassophlebia* is then also known from the German Hettangian and the family ranges to the Kyrgyz Pliensbachian/Toarcian and the German Toarcian.

Campterophlebiidae is first recorded in the Hettangian when it is known from both England (*Petrophlebia* and *Archithemis*) and China (*Dorsettia*). *Petrophlebia* is unknown after the Hettangian but *Archithemis* survived until the Toarcian and is also known from the German Toarcian suggesting that it migrated eastwards in the Early Jurassic. *Dorsettia* apparently originated in the Chinese Hettangian and then migrated westwards as it is also recorded in the English Sinemurian suggesting large geographic ranges in the Early Jurassic but not the Late Triassic.

5.4.5 Hemiptera

Most genera of bugs from the TJB of Britain, except *Procercopis*, are monotypic and those recorded in the Rhaetian are not known again after the TJB. *Protocoris indistinctus* is the only species recorded in the Hettangian, its first and last appearance in the record. There are two other occurrences though in two families—Belostomatidae and Archijassidae—that are not identified to genus or species level but indicate slightly higher abundance than the species data alone would suggest. However, compared to 13 occurrences of eight species from the Rhaetian and 17 occurrences of 10 species from the Sinemurian this suggests a major lull in hemipteran diversity in the Hettangian. The data suggest that Dysmorphoptilidae suffered quite extensively at the TJB becoming rare in the Early Jurassic but persisting to the Middle Jurassic of China (Lin, 1986) and even the genus *Dysmorphoptila* persisted to the Middle Jurassic of Mongolia (Shcherbakov, 1988). Conversely, Procercopidae appears to have been rare in the Late Triassic becoming more widespread in the Early Jurassic.

5.4.6 Other orders

Dermaptera.—Earwigs are known from three genera, only one of which crosses the TJB. *Phanerogramma heeri* is recorded from the Rhaetian and Hettangian but declines in abundance across the boundary. Earwigs are exceedingly rare in the global dataset with only four other species described. Two are described in the genus *Baseopsis* from the Swiss Hettangian (*B. forficulina*) and the

Russian Toarcian (*B. sibirica*). The other two were described for this project (Kelly et al., 2018b) from the Australian Norian, also in *Phanerogramma*, suggesting that this genus had a very wide geographic range stretching from western Tethys to the south-eastern tip of Pangea. The other species are only known from the English Sinemurian (*Brevicula gradus* and *B. maculata*) and the Toarcian (*Trivenoptera moorei*) but may be more widespread. *Brevicula* may also be present in the Chinese Hettangian/Sinemurian Badaowan Formation (personal observation of collections at NIGPAS), and *Trivenoptera* and *Phanerogramma* may be present in the German Toarcian "Green Series" (personal observation of collections in Germany held by Jörg Ansorge).

Trichoptera.—Caddisflies are known from one monotypic genus in both the Rhaetian and Hettangian (*Austaulius furcatus*), which crossed the TJB but is unknown after the Hettangian. *A. haustrum* is only known from the Sinemurian and *Necrotaulius parvulus* is only known from the Toarcian. Prior to taxonomic revision this order was more speciose as three species were synonymised with *A. furcatus* (Kelly et al., 2018a). However, of these only *N. apicalis* was from a known locality and so could be aged to the Hettangian. Even so, this additional species in the Hettangian would have suggested an increase in diversity across the TJB. There is no evidence for a shift in geographic range or radiation in the Early Jurassic. *Necrotaulius* is also recorded in the Kyrgyz Carnian and the German Toarcian suggesting a large stratigraphic and geographic range but there is no evidence of further radiations or migrations in the Early Jurassic.

Neuroptera.—Lacewings are known from four genera, two of which crossed the TJB. *Archeosmylus* is known from one species (*A. complexus*) which crossed the TJB ranging through to the Toarcian. *Prohemerobius* also crossed the boundary but the Rhaetian species, with 'Neur:Proh.sp.nov.2' going extinct at the TJB. Then there was a lull for the genus until the Toarcian when *P. aldertonensis* is recorded. The genus is always rare, being known from only one specimen of each species. *Megapolystoechus* is known from one species, *M. magnificus*, which is unknown after the TJB and *Actinophlebia* is first recorded in the Hettangian with "Neur:Proh. sp. nov. 1" and ranges to the Toarcian when *A. intermixta* is also recorded.

Blattodea.—There are seven monotypic genera of cockroaches described from the English material. The two recorded in the Rhaetian (*Rhiphidoblattina* and *Actinoblattula*) are unknown after the TJB. There is only one occurrence record for a cockroach in the English Hettangian (*Mesobattina* sp.). Then by the Sinemurian they appear to recover, with two new genera recorded. There is a project planned to describe the newly discovered cockroaches lead by andrew Ross, but it was not possible to start it during the current project due to time restraints.

Diptera.—Similarly, with the true flies, there are nine monotypic genera described and the two recorded in the Rhaetian (*Aenna* and *Rhaetania*) are unknown after the TJB. There are no occurrences recorded from the Hettangian, then four genera are recorded from the Sinemurian. This is further evidence for an impoverished Hettangian fauna.

There are problems associated with scaling between local, regional, and global scales, as it becomes more difficult to revise the data to improve accuracy, but the global dataset is more abundant and stratigraphically complete than the UK or NWT datasets and therefore allows for statistical correction of potential sampling biases. The species level remains difficult to work with due to the high number of single-occurrence, single-collection, and single-interval species. This is also a problem at genus level, but it is not so pronounced. This introduces problems with many statistical methods. Large-scale compilation analyses of insect occurrence will greatly benefit from increased reporting of insect taxa, not only descriptions of new taxa. The genus-level data was statistically corrected and provided a more robust analysis of diversity dynamics through the whole interval of interest and suggests a decline across the TJB, that may be extended back to the Norian. The dataset also picked up on declines in diversity in the Carnian and the Toarcian consistent with reports of extinction events at these times (Aberhan and Fursich, 2000; Benton et al., 2018).

5.5 Concluding remarks

For the present study, an occurrence-based dataset was compiled to examine the diversity dynamics of insects through the Late Triassic and Early Jurassic to determine whether there was an extinction event for insects in the Late Triassic. Previous studies have not detected such an event but usually analysed diversity only at family level. Family-level taxonomy is much more stable than genus or species level and is more statistically sound than genus- or species-level data but may not be ideal for detecting insect extinctions. Insect families can be vast and incredibly diverse, with some beetle families having tens of thousands of species and varied ecological functions and so would be expected to survive most periods of environmental perturbation, even if there was a massive decline in species or genera. To improve the dataset there was a period of taxonomic revision focusing on the British insects as they provide the best record of insect occurrence across the TJB and stratigraphic revision of all known insect-bearing horizons globally. Based on this dataset, insect diversity was investigated at a range of taxonomic, stratigraphic, and geographic scales, although not all levels of analyses have sufficient data to offer confident results. Although there are problems with the dataset, including a high abundance of single-interval taxa and stratigraphic/geographic gaps, the present study provides compelling evidence for an extinction event for insects between the Late Triassic and Early Jurassic

from an in-depth assessment of species- and genus-level turnover in the UK and a global genus-level analysis of diversity metrics through the Late Triassic/Early Jurassic. Ecosystem restructuring is evident with some orders declining heavily (beetles and bugs), some almost completely (cockroaches and true flies), and some seemingly benefitting (crickets). A large increase in orthopterans may be evidence for outbreaks, but it is peculiar that this is observed in the Hettangian.

According to the data, there was a loss of overall richness of insect genera and species across the TJB at all geographic scales and at both stage and substage levels. In the UK, at stage level there was a 43% drop in genera and a 51% drop in species richness; for the NWT region there was a 21% of genera and 29% of species; and at GL level there was a 19% drop in genera and a 31% drop in species. The GL genus-level data allowed for statistical correction, which suggested a 58% drop in genus richness across the RJB. The most reliable results presented were considered to be those of the global genus-level analysis as this was the only data robust enough to statistically correct. Whereas, the species and substage level data were restricted by almost ubiquitous single-interval species and numerous substages with zero data. Different methods for treating occurrences of unsure age introduced massive changes to diversity curves between the different methods (removal, inclusion in all, randomly assigned) indicating that these data are important for establishing substage-level dynamics through the interval of interest and should be developed further to this end. This is not surprising given that formations of uncertain substage account for almost half of occurrences in the global dataset, mostly the Central Asian material. As these formations continue to be assessed and methods for correlating terrestrial sections with global standards based on marine sections improve so will our estimates for the ages of the insect-bearing horizons from this region.

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Appendix 1. KELLY, R. S. and NEL, A. 2018. Revision of the damsel-dragonfly family Campterophlebiidae (Odonata) from the Early Jurassic of England reveals a new genus and species, Alcheringa 42:87–93.

Revision of the damsel-dragonfly family Campterophlebiidae (Odonata) from the Early Jurassic of England reveals a new genus and species

RICHARD S. KELLY and ANDRÉ NEL

KELLY, R.S. & NEL, A., October 2017. Revision of the damsel-dragonfly family Campterophlebiidae (Odonata) from the Early Jurassic of England reveals a new genus and species. *Alcheringa 42*, 87–93. ISSN 0311-5518.

Historical fossil insect collections from England were re-examined and the taxa revised. *Lateophlebia* gen. nov. is erected for *Liassophlebia anglicanopsis* (Zeuner) in Campterophlebiidae. *Petrophlebia anglicana* Tillyard is confirmed in this family and *Archithemis liassina* (Strickland) is transferred to this family. Lastly, *Archithemis brodiei* (Geinitz), *Archithemis* Handlirsch, and Architemistidae Tillyard (reduced to this sole species) are transferred to the Heterophlebioidea.

Richard Kelly [richard.kelly@bristol.ac.uk], School of Earth Sciences, University of Bristol, Life Sciences Building, 24 Tyndall Avenue, Bristol, BS8 1TQ, UK; Department of Natural Sciences, National Museum of Scotland, Chambers Street, Edinburgh, EH1 1JF, UK. André Nel [anel@mnhn.fr], Institut de Systématique, Évolution, Biodiversité, ISYEB—UMR 7205—CNRS, MNHN, UPMC, EPHE, Muséum national d'Histoire naturelle, Sorbonne Universités, 57 rue Cuvier, CP 50, Entomologie, F-75005, Paris, France. *Received 26.4.2017; revised 24.7.2017; accepted 6.9.2017.*

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THE DAMSEL-DRAGONFLY family Campterophlebiidae is known from deposits ranging in age from the Late Triassic of Krygyzstan (Pritykina 1970) to the Early Cretaceous of China (Li *et al.* 2012a) and Russia (Pritykina 2006), and is relatively common in Jurassic assemblages from England, Germany, Kyrgyzstan, China and Russia (Nel *et al.* 1993, Nel & Weiss 2017). This family is currently represented in England by *Petrophlebia* Tillyard, 1925 (see below), *Dorsettia* Whalley, 1985, which had a wide geographical range also being found in northwestern China (Zheng *et al.* 2016) and *Hypsothemis* Pritykina, 1968 (*H. fraseri* Whalley, 1985).

Historical collections of English fossil insects from the Late Triassic and Early Jurassic have been re-examined and the taxa revised leading to the discovery of new taxa and the synonymisation of other taxa. In this paper we revise representatives of Campterophlebiidae, holotypes are redrawn and revised and non-holotype material is surveyed leading to the establishment of a new genus of damsel-dragonfly in this family. Additionally, we discuss the familial placement of *Petrophlebia*. Presently, the genus is assigned to Campterophlebiidae, but Bechly (2016) suggested that it should be transferred back to Architemistidae where it was placed by Fraser (1957).

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Geological setting

The specimens discussed are from the Early Jurassic: lower Lias of England and are, therefore, *ca* 190 million years old. The lower Lias in the midlands and south of England consists of the Blue Lias Formation, which spans from the Triassic/Jurassic boundary to the lower Sinemurian, and it is overlain by the Charmouth Mudstone Member, which extends into the Pliensbachian (Simms *et al.* 2004).

The specimen from Barrow-upon-Soar, Leicestershire (National Grid Reference SK 575 175) is Hettangian in age, being found in the Planorbis Chronozone (Blue Lias Formation: Wilmcote Limestone Member). The specimens from Stonebarrow, Dorset (SY 369 929) are from the slightly higher Sinemurian stage. They were collected from the 'flatstones', which is a local name for a horizon found in bed 83/83 h of the Obtusum Chronozone: Obtusum Subchronozone (Charmouth Mudstone Formation, Black Ven Mudstone Member) (Page 2010). The Stonebarrow site was discussed in more detail by Kelly *et al.* (2017); for an in-depth description of the stratigraphy of the Dorset coast Lias, see Page (2010); the Barrow-upon-Soar locality was discussed by Martin *et al.* (1986).

Fig. 1. Location of collection sites discussed from England: 1. Barrow-upon-Soar, Leicestershire; 2. Stonebarrow, Dorset. Map in figure 1 was adapted from d-maps.com.

Materials and methods

The material is held in the collections of the Natural History Museum, London (NHMUK) and the Warwickshire Museum, Warwick (WARMS). The Dorset specimen is part of the Jackson collection from the Jurassic Coast of England (Fig. 1) collected in the mid-twentieth century, and the Leicestershire specimen is part of the Edgell collection from the late nineteenth century. The specimens were examined first-hand by the primary author and remotely by the co-author. They were examined dry using a light stereomicroscope. Photographs were taken under alcohol, where possible, using a Nikon D3300 with an AF-S Micro Nikkor 40 mm macro lens attached to a stand.

The venation nomenclature is based on the interpretations of Riek & Kukalová-Peck (1984), as modified by Nel *et al.* (1993) and Bechly (1996). The abbreviations are as follows: AA, anterior anal; AP, posterior anal; Ax, primary antenodal cross-vein; Arc, arculus; CuAa, distal branch of anterior cubitus; CuAb, proximal branch of anterior cubitus; CuP, posterior cubitus; DC, discoidal cell; MAa, anterior branch of anterior median; Mab, posterior branch of anterior median; MP, posterior median; RA, anterior radius; RP, posterior radius; ScP, posterior subcostal; IR, intercalary vein; 'O', oblique vein; Pt, pterostigma; T, triangle; Ht, hypertriangle, N, nodus. The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly (1996, 2016). Taxonomic figures were constructed in Serif DrawPlus X6.

Systematic palaeontology

Class INSECTA Linnaeus 1758
Order ODONATA Fabricius 1793
Clade ISOPHLEBIOPTERA Bechly 1996
Subclade ISOPHLEBIIDA Bechly 1996
Superfamily ISOPHLEBIOIDEA Handlirsch 1906
Family CAMPTEROPHLEBIIDAE Handlirsch 1920

Lateophlebia gen. nov.
Type species. *Lateophlebia anglicanopsis* (Zeuner, 1962).

Etymology. 'Lateo' is the Latin word for hidden, and 'phlebia' is a common odonatan suffix.

Diagnosis. Hindwing characters only (probably female owing to lack of anal angle and triangle). Anal vein completely separated from CuA; subdiscoidal area posteriorly open; CuAb distinctly curved; CuAa ending well distal of bases of RP3/4 and IR2, and basal of nodus level; RP3/4 and MAa nearly straight.

Lateophlebia anglicanopsis (Zeuner 1962)

1962 *Petrophlebia anglicanopsis* Zeuner, pp. 160–161, pl. 24, figs 1–2.
1985 *Liassophlebia anglicanopsis* (Zeuner, 1962); Whalley, pp. 122–123, fig. 8a.
1993 *Liassophlebia anglicanopsis* (Zeuner, 1962); Nel *et al.*, pp. 141–142.

Holotype. NHMUK In.49573 (Fig. 2).

Locality and age. Stonebarrow, Dorset. Sinemurian ('Flatstones', Bed 83, Obtusum Chronozone: Obtusum Subchronozone).

Diagnosis. Female hindwing; areas between CuAa and MP and between MP and MAa narrow; mostly only one row of cells in areas between MAa and MP, and between MP and CuAa; very few cells in subdiscoidal area below discoidal cell.

Redescription. This species is based on basal two-thirds of a single hindwing. Wing hyaline, preserved part 67.5 mm long and 20.0 mm wide. Distance between base and arculus 10.0 mm and between arculus and nodus 28.5 mm. Wing shortly petiolate; anal area poorly preserved but with irregular cells, some smaller than others; median space free, submedian space with curved vein CuP; curved cross-vein separates submedian and subdiscoidal spaces; subdiscoidal space posteriorly open and transverse, with AA making sub-right angle in basal part.

Discoidal cell free, closed basally, narrowly elongate, 3.5 mm long and 1.7 mm wide; RP and MA strongly separated at arculus; MAb less than twice as long as basal side of discoidal cell, which is 1.0 mm long; MAb well aligned with distal free part of CuA.

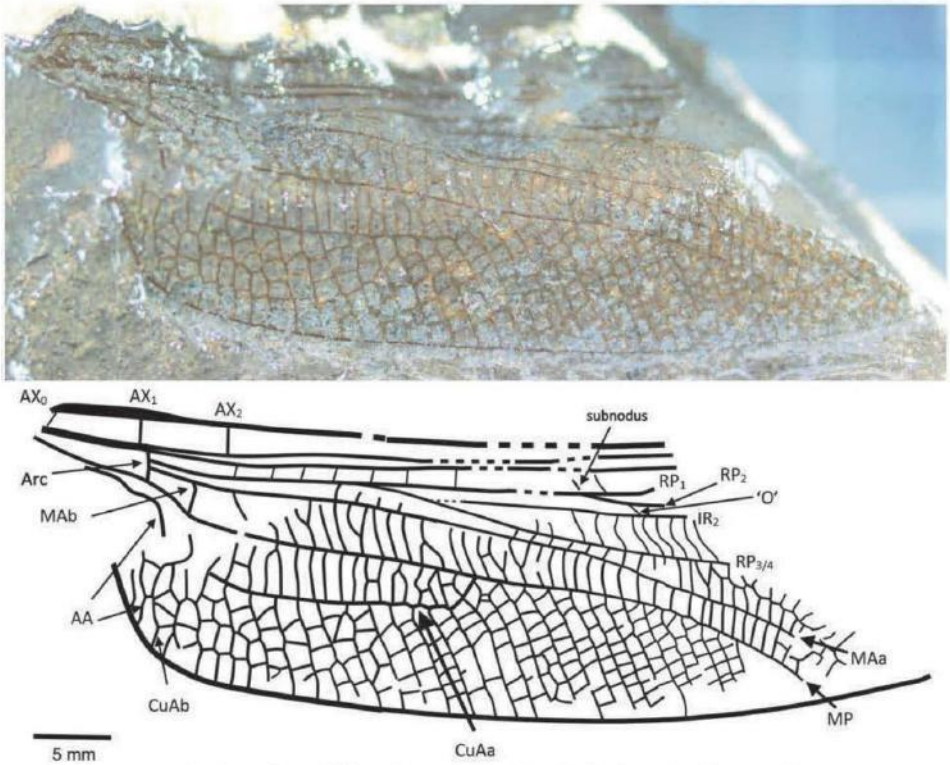

Fig. 2. Holotype of *Lateophlebia anglicanopsis* (NHMUK In.49573), photograph and reconstruction.

Distal free part of CuA is 3.5 mm long, dividing into CuAa and CuAb; CuAb 6.2 mm long, curved, directed towards posterior margin. CuAa relatively short, ending well basal of nodus level, with 12 posterior branches. CuAa and MP well-separated, clearly parallel for a long distance, one row of intervening transverse cells. Area between MP and CuAa 4.0 mm wide; MP weakly curved, reaching posterior margin well distal of nodus level, 61.2 mm from wing base; MAa nearly straight, more or less parallel to MP, with one row of cells in basal part of postdiscoidal area, 4.0 mm wide, narrower than area between MP and CuAa.

Postdiscoidal area becoming narrower below nodus but broader near posterior wing margin with four rows of small cells present; Ax0 visible, very near to wing base; two primary antenodal veins very strong, Ax1 1.2 mm basal of arculus and Ax2 5.7 mm distal of arculus, Ax1 nearly perpendicular to ScP and R+MA, Ax2 more oblique; no secondary antenodal cross-vein visible; about seven preserved antesubnodal cross-veins between arculus and subnodus; base of RP3/4 10.5 mm distal of arculus, closer to arculus than to nodus; base of IR2 very close to that of RP3/4, 2.5 mm distally, originating distinctly from RP; nodal crossing and subnodus oblique; postnodal and postsubnodal cross-veins not preserved; RP2 aligned with subnodus; first oblique vein 'O' two cells and 3.7 mm distal of base of RP2; area between MAa and RP3/4 widened distally; area between RP3/4 and IR2 strongly widened distally.

Remarks. *Lateophlebia anglicanopsis* differs greatly from the hindwings of Heterophlebiomorpha (including those of Liassophlebiidae) in the shape of the discoidal cell, which is narrowly elongate, with posterior side straight and distal side not twice as long as basal side. Neither is there a cross-vein, complete or incomplete, in the discoidal cell. Furthermore, the shape of the cubito-anal area differs strongly from those in Heterophlebiomorpha. Vein AA is not fused with CuA, and the area between MP and CuAa is broader than the postdiscoidal area. These characters are apomorphies of Isophlebioidea. Thus, this species does not belong to *Liassophlebia*.

The species was originally attributed to *Petrophlebia* (placed here in the isophlebiomorphan family

Architemistidae Tillyard 1917; see below). However, it differs from *Petrophlebia* and Architemistidae in the veins AA and CuAb being completely separated. Within Isophlebioidea, *Lateophlebia* can be attributed to Campterophlebiidae rather than to Isophlebiidae based on the following characters: opposite curvature of MA and MP constricting the area between them (apomorphy); basal part of area between MP and CuAa less than twice as wide as basal part of area between MAa and MP (plesiomorphy); distal side (MAb) of discoidal cell and gaff (basal CuA before its furcation) not orientated in one transverse axis (plesiomorphy).

Within Campterophlebiidae, *Lateophlebia* belongs to the group of genera that have the AA vein completely separated from CuA so that the subdiscoidal area is open posteriorly, viz., *Campterophlebia* Bode, 1905, *Pritykinia* Nel *et al.*, 2009, *Piernopteron* Pritykina, 1970, *Oreophlebia* Pritykina, 1985, *Amnifleckia* Zhang *et al.*, 2006, *Qibinlina* Nel *et al.*, 2009, *Dorsettia* Whalley, 1985, and *Gallodorsettia* Nel & Weis, 2017, plus possibly *Sibirioneura* Pritykina, 1985 (Nel *et al.* 1993, 2009, Zhang *et al.* 2006, Zheng *et al.* 2016, Nel & Weis 2017).

Lateophlebia differs from *Gallodorsettia* and *Oreophlebia* in the distinctly curved CuAb and narrower areas between CuAa and MP, and between MP and MAa. *Lateophlebia* differs from *Dorsettia*, *Amnifleckia*, *Qibinlina* and *Piernopteron* in the longer CuAa, which ends distal to the bases of RP3/4 and IR2. It also differs from *Sibirioneura* in the nearly straight RP3/4 and MAa. All these characters are shared with *Campterophlebia* but it differs from this genus in the presence mostly of a single row of cells in the areas between MAa and MP, and between MP and CuAa, plus the presence of very few cells in the subdiscoidal area below the discoidal cell, as in *Pritykinia*. *Lateophlebia* differs from *Pritykinia* in the curved MAb and the presence of only one row of cells in the area between CuAa and MP. Therefore, we consider that it corresponds to a new genus.

A second specimen (NHMUK In. 59376) was attributed to *Petrophlebia anglicanopsis* by Zeuner (1962). However, this specimen corresponds to the distal half of a wing and, therefore, there is little similarity with the holotype (basal portion). This fossil is probably referable to Campterophlebiidae, as there is a long pterostigma present, which is basally recessed, but its attribution to the same species is questionable.

Petrophlebia Tillyard 1925
Type species. *Petrophlebia anglicana* Tillyard, 1925

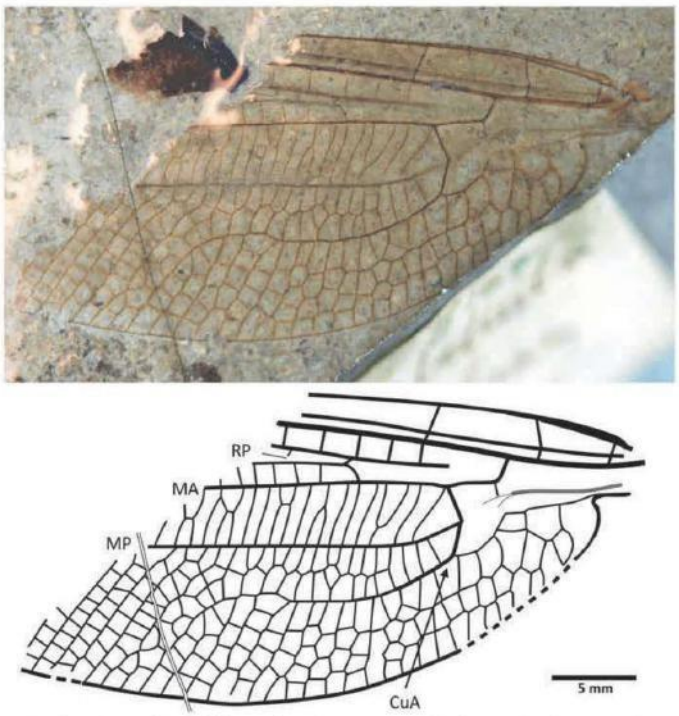

Fig. 3. Holotype of *Petrophlebia anglicana* (NHMUK I.10494), photograph and reconstruction.

Petrophlebia anglicana Tillyard 1925

1925 *Petrophlebia anglicana* Tillyard, p. 13, pl. 1, fig. 2, text-fig. 2.
1993 *Petrophlebia anglicana* Tillyard; Nel *et al.*, p. 236, fig. 195.
2011 *Petrophlebia anglicana* Tillyard; Petrulevičius *et al.*, p. 736.
2012b *Petrophlebia anglicana* Tillyard; Li *et al.*, p. 66.

Holotype. NHMUK I.10494 (Fig. 3).

Locality and age. Barrow-upon-Soar, Leicestershire; Hettangian (Planorbis Chronozone).

Remarks. This taxon was originally placed in Liassophlebiidae but was later transferred to Architemistidae Tillyard 1917 by Fraser (1957); and then Campterophlebiidae by Nel *et al.* (1993) where it was retained by Petrulevičius *et al.* (2011). Bechly (2016) proposed to restore it to Architemistidae on the basis of two putative synapomorphies: a single row of very long transverse and oblique cross-veins in the postdiscoidal area of the hindwing and IR2 originating on RP3/4. The first character is of relatively little value because it is also present in some campterophlebiid genera, e.g. *Sogdophlebia*, *Angaroneura* and *Sibirioneura amurica*. The second character is of greater value because it is more rarely distributed in these Odonata. Moreover, the comparable parts of the hindwing venation of *Petrophlebia anglicana* and of *Archithemis liassina* (Strickland, 1840) (after the reconstruction proposed by Tillyard 1917) are nearly identical. However, the holotype of *A. liassina* (specimen WARMS G 307 from the Hettangian Planorbis Chronozone of Nook quarry, Bickmarsh, Warwickshire) is rather poorly preserved (Fig. 3). If what is now visible is congruent with the characters of *Petrophlebia*, the most important structures are very poorly visible.

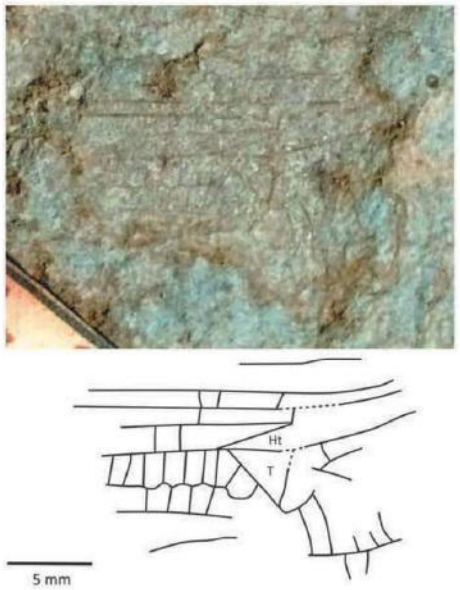

Fig. 4. Holotype of *Libellula* (*Aeschna*) *brodiei* (WARMS G 8079), photograph and reconstruction.

The type species *Architemis brodiei* (Geinitz, 1884) of Architemistidae was originally named *Libellula* (*Aeschna*) *brodiei*, and designated after the original figure of Brodie (1845, pl. 8, fig. 1). Handlirsch (1906–1908, pl. 42, fig. 1) later considered it as the type species of *Architemis* Handlirsch, 1906–1908. The specimen was figured by Brodie (1845, pl. 8, fig. 1) under the label '*Libellula Brodiei* (Buckman. Geol. Proc. vol. iv. p. 211), Upper Lias, Dumbleton', yet the figure by Handlirsch (1906–1908) shows a discoidal cell divided into a hypertriangle and a triangle by a cross-vein, IR2 on RP3/4 is not branched, and a subdiscoidal space is present, which is very similar to those of Heterophlebiomorpha, and not to those of Isophlebioptera. The specimen in Brodie's figure was found to correspond to the specimen WARMS G 8079 (Fig. 4). Buckman (1843, p. 212) indeed named a fossil *Libellula* (*Aeschna*) *brodiei* from the county of Gloucestershire, but without describing it. Tillyard (1917, fig. 157) figured (apparently after Handlirsch) the basal part of the wing with structures completely different, viz., a one-celled discoidal rectangle, IR2 beginning on RP3/4 and a subdiscoidal cell of isophlebiopteran type.

It is clear from the photograph of the holotype of *Libellula* (*Aeschna*) *brodiei* (Fig. 4) that the specimen is a hindwing with a clear division of the discoidal space into a hypertriangle and a discoidal triangle, plus a subdiscoidal space of the heterophlebioid type. This fossil seems to have no supplementary antenodal cross-veins in the space between C and ScP, which would suggest a position in Heterophlebiidae. Nevertheless, this fossil is too incomplete to allow a precise comparison with the other taxa in this family. As a result, *Architemis brodiei* is a Heterophlebioidea incertae sedis. *Architemis* and Architemistidae must be transferred to this superfamily.

Brodie (1845, pl. 10, fig. 4) figured another hindwing that corresponds exactly to the pattern of venation of *Petrophlebia* and was named by Brodie as 'Wing of Mr. Strickland's *Aeschna liassina* drawn from the original', which corresponds to the original figure of Strickland (1840, fig. 11). *Archithemis liassina* (Strickland, 1840) differs markedly from *Archithemis brodiei* in the absence of division of the discoidal space into a hypertriangle and a triangle (Fig. 5). Thus, it does not belong to Heterophlebioidea. It does not belong to *Archithemis* and Architemistidae, which must be reduced to the sole *Architemis brodiei*, as *Petrophlebia anglicana* is referable to Campterophlebiidae (see above). *Archithemis liassina* also belongs to Campterophlebiidae, but its

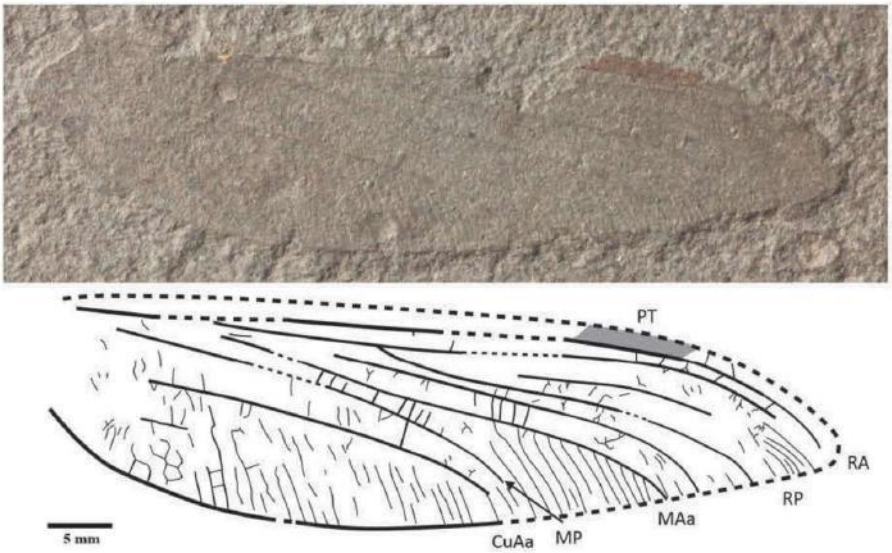

Fig. 5. Holotype of '*Archithemis liassina*' (WARMS G 307), photograph and reconstruction.

exact generic position remains uncertain because of its poor preservation.

Discussion

Lateophlebia is the fourth and one of the oldest representatives of Campterophlebiidae in the Liassic of Europe, after *Campterophlebia* and *Gallodorsettia* from the Toarcian of Germany and the Grand-Duchy of Luxembourg, and *Dorsettia*, which is contemporaneous with *Lateophlebia* also found in the 'flatstones' of Stonebarrow (Whalley 1985). All European specimens were collected from facies associated with shallow marine palaeoenvironments. In contrast, campterophlebiids from Asia were preserved in deposits associated with freshwater environments, and are much more common and diverse.

As well as describing *Lateophlebia* in Campterophlebiidae in this paper, we have discussed the status Archithemistidae. Based on the holotype of the type species *Archithemis brodiei* it is clear from the preserved characters that it is closer to Heterophlebiomorpha, and not to Isophlebioptera. However, owing to the poor preservation of the specimen, it has been designated as Heterophlebioidea incertae sedis, and the genus and family transferred to this superfamily.

Data access statement

This study did not involve any underlying data. All specimens are available for re-study in the public institute indicated in the text.

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The lead author would like to acknowledge the support of his PhD supervisors Mike Benton, at the University of Bristol, and Andrew Ross, at the National Museum of Scotland, for their advice and support throughout his PhD project. The authors would also like to thank Claire Mellish, the curator of invertebrate palaeontology at the NHMUK, for access to the collections, and Jon Radley, at WARMS, for access to the collections and for photographs of the specimens in his care. Also thanks to the Natural Environment Research Council for funding the lead author's PhD project from which this study was made possible (studentship number: NE/L002434/1).

Disclosure statement

No potential conflict of interest was reported by the authors.

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Appendix 2. KELLY, R. S. and NEL, A., 2018. Revision of some damsel-dragonflies (Odonata, Liassophlebiidae and Anglophlebiidae new family) from the Triassic/Jurassic of England and Antarctica. Journal of Paleontology, 92:1035–1048.

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Revision of some damsel-dragonflies (Odonata, Liassophlebiidae and Anglophlebiidae new family) from the Triassic/Jurassic of England and Antarctica

Richard S. Kelly,[1,2] and André Nel[3]

[1]School of Earth Sciences, University of Bristol, Life Sciences Building, 24 Tyndall Avenue, Bristol, BS8 1TQ, England
[2]Department of Natural Sciences, National Museum of Scotland, Chambers Road, Edinburgh, EH1 1JF, Scotland, United Kingdom ⟨richard.kelly@bristol.ac.uk⟩
[3]Institut de Systématique, Évolution, Biodiversité, ISYEB - UMR 7205 – CNRS, MNHN, UPMC, EPHE, Muséum National d'Histoire Naturelle, Sorbonne Universités, 57 Rue Cuvier, CP 50, Entomologie, F-75005, Paris, France ⟨anel@mnhn.fr⟩

Abstract.—Fossil insects from the Triassic-Jurassic boundary of England could provide an important resource for investigating the severity of extinction events in the terrestrial realm of the uppermost Triassic. However, the fossil record is poorly understood for this period even though there are abundant historical collections. Many of these collections are still in need of taxonomic revision before they can be used to reconstruct past entomofaunas and make inferences about diversity change through time. This paper is part of a larger project to revise the taxonomy of insects across the Triassic-Jurassic boundary of England to better understand changes in insect diversity through the Triassic-Jurassic boundary and associated extinction period. Herein, the damsel-dragonfly family Liassophlebiidae Tillyard, 1925 is revised and an additional specimen from the Early Jurassic of Antarctica is included. *Rossiphlebia* new genus is erected for *Liassophlebia jacksoni* Zeuner, 1962; *L. batheri* Tillyard, 1925 is considered nomen dubium and another specimen originally attributed to *L. batheri* is identified as *L. withersi* Tillyard, 1925. *Liassophlebia* (?) *clavigaster* Tillyard, 1925 and *L.* (?) *hopei* (Brodie, 1845) are considered incertae sedis at the generic level. *Liassophlebia gigantea* Zeuner, 1962 is based on a fragmentary specimen but has several unique key characteristics. We redescribe it in *Anglophlebia* new genus and tentatively in Anglophlebiidae new family in Heterophlebioptera. Also discussed are *L. magnifica* Tillyard, 1925, *L. withersi*, and *L. pseudomagnifica* Whalley, 1985, which are redescribed with updated figures. *Caraphlebia antarctica* Carpenter, 1969 was originally described from the Early Jurassic of Antarctica as being closely related to *Liassophlebia*; it is herein confirmed in Selenothemistidae Handlirsch, 1939.

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Introduction

The Late Triassic saw several periods of major biodiversity turnover, culminating in the End Triassic Extinction (ETE), described as one of the five largest mass extinction events in Earth history. Studies have suggested that >50% of genera from marine and terrestrial environments (Deenan et al., 2010), 23.4% of marine families, and 21.7% of terrestrial families (McGhee et al., 2004) went extinct (although insects were not counted in these studies). Nevertheless, there are current discussions on the severity of this event and whether it was one event or drawn out throughout the Rhaetian. The effects of this period on insect diversity are not well studied and large-scale datasets of insect diversity through time tend not to show an extreme event at the Triassic-Jurassic Boundary (TJB) (see Nicholson et al., 2015; Condamine et al., 2016). This paper is part of a larger study investigating the changes in insect diversity across the TJB to assess the impact of the ETE on insect diversity. Because there are few currently available rich insect outcrops, a large part of this project is the taxonomic revision of historical fossil insect collections from the Late Triassic to Early Jurassic at the species level to bring the taxonomy to current understanding. Herein, we revise Liassophlebiidae Tillyard, 1925, a family of damsel-dragonflies known from the Late Triassic and Early Jurassic of Europe, Central Asia, China, and Antarctica.

Liassophlebiidae is a small extinct family of damsel-dragonflies known from the early Mesozoic of western Europe, Central Asia, and Antarctica described in the suborder Epiprocta, which contains the extant dragonflies, similar in form to the other extant odonate suborder Zygoptera (damselflies). Most species are described from isolated wings or abdominal segments of adults and there are no known larval specimens, although it is difficult to compare adult and larval fossil specimens because they are so different morphologically. Only *Liassophlebia* Tillyard, 1925 and *Petrophlebia* Tillyard, 1925

(type species *P. anglicana* Tillyard, 1925) were included in the family by Tillyard (1925). *Liassophlebia* originally comprised four species based on wings: *L. magnifica* Tillyard, 1925, *L. batheri* Tillyard, 1925, *L. withersi* Tillyard, 1925, and *L. westwoodi* (Hagen, 1850), and two possible species based on partial abdomens: *L.* (?) *clavigaster* Tillyard, 1925 and *L.* (?) *hopei* (Brodie, 1845). *Liassophlebia westwoodi* was described from a specimen previously figured by Brodie (1845, pl. 10, fig. 8) and named *Heterophlebia westwoodi* by Hagen (1850, p. 359); it was later transferred to *Tarsophlebia* Hagen, 1866 by Hagen (1866). *Liassophlebia* (?) *hopei* was described from a specimen figured and named *Libellula hopei* by Brodie (1845, pl. 10, fig. 3); it was later transferred to *Heterophlebia* Westwood, 1849 by Selys-Longchamps and Hagen (1850) and then '(Anisozygopteron?)' by Handlirsch (1906). *Petrophlebia* was transferred to Architemistidae Tillyard, 1917 by Fraser (1957) and then to Campterophlebiidae Handlirsch, 1920 by Nel et al. (1993). Although Bechly (2016) proposed to transfer it back to Architemistidae, its position in the Campterophlebiidae was confirmed by revision of the family by Kelly and Nel (2017).

The diagnosis of Liassophlebiidae was slightly emended by Zeuner (1962) to include species with a discoidal cell closed basally. *Petrophlebia anglicanopsis* Zeuner, 1962, *Liassophlebia jacksoni* Zeuner, 1962, and *L. gigantea* Zeuner, 1962 were also described. Additional specimens were identified as *L. magnifica* from the Jackson collection of the lower Lias of Dorset. The Jackson collection was re-examined by Whalley (1985) who altered some of Zeuner's species descriptions, transferred *P. anglicanopsis* to *Liassophlebia* and described *L. pseudomagnifica* Whalley, 1985 from one of Zeuner's *L. magnifica* specimens. *Liassophlebia anglicanopsis* was considered an uncertain taxon in Liassophlebiidae by Nel et al. (1993).

Additional genera were included from continental Europe, Central Asia, China, and Antarctica, which are not known from the British deposits: (1) *Caraphlebia* Carpenter, 1969 from South Victoria Land, Antarctica was considered possibly referable to Turanothemistidae Pritykina, 1968 by Nel et al. (1993) but was transferred to Selenothemistidae Handlirsch, 1939 by Bechly (2016); (2) *Ferganophlebia* Pritykina, 1970 from the Early Jurassic of Kyrgyzstan; (3) *Paraliassophlebia* Hong, 1983 from the Middle Jurassic of China was considered as Epiprocta incertae sedis by Nel et al. (1993) but was tentatively transferred to Selenothemistidae by Bechly (2016); and (4) *Grimmenopteron* Ansorge, 1996 and *Bavarophlebia* Nel and Petrulevičius, 2005, both from the Toarcian of Germany, each with one associated species. A further specimen was identified as *Liassophlebia* sp. from the Early Jurassic of Austria by Kohli et al. (2016).

Liassophlebiidae was reported to be known from the Early Jurassic, Hettangian-Toarcian, by Nicholson et al. (2015, supplementary data) but this disregards the four species described by Tillyard (1925) from the Penarth Group of Strensham, England, which is Late Triassic: Rhaetian. This locality was reported as Rhaetian by Nicholson et al. (2015) for other families but Tillyard's book was not cited so these species must have been missed. The inclusion of this omission changes the dynamics of the family across the TJB because including these four species extends the family to before the boundary, indicating that the family survived the extinction event rather than originating in the subsequent stage.

Geological setting

The specimens discussed herein are from the Late Triassic to Early Jurassic of England (Fig. 1). They are mostly found in shallow marine limestones; these rocks are fine-grained enough to generally preserve insects well. The living insects were not necessarily associated with the marine environment but were transported from their terrestrial or freshwater habitat through fluvial systems to their final deposition in the marine shallows. The Late Triassic material was collected from bed 18 of the Penarth Group at the historical locality of Strensham in the county of Worcestershire (Brodie, 1845) and was updated to current geological nomenclature by Kelly et al. (2017) who found the horizon to lie within the Lilstock Formation, Cotham Member, which is Rhaetian in age. The Early Jurassic fossils were collected from three localities Binton in the county of Warwickshire, another historical locality, exposed several insect-bearing horizons, which Brodie (1845) originally described and Kelly et al. (2018) found to correspond to the Planorbis Chronozone (Blue Lias Formation, Wilmcote Limestone Member) of the Hettangian. The other two localities—Stonebarrow and Catherston Lane—are very similar and are found at or near the Dorset coast. Stonebarrow is still actively collected from and Catherston Lane was active for a short time during the construction of the Charmouth bypass. There are several insect-bearing horizons; the insects discussed herein were collected from the 'flatstones' (bed 83/83h), which is a local name for a horizon found in the Obtusum Chronozone, Obtusum Subchronozone (Charmouth Mudstone Formation, Black Ven Mudstone Member) (Page, 2010; Kelly et al., 2017).

Caraphlebia antarctica Carpenter, 1969 was described from the Jurassic 'Mawson Tillite' on Carapace Nunatak, South Victoria Land, Antarctica (Carpenter, 1969). Mawson Tillite is a historical name for the Mawson Diamictite of the Ferrar Group (Balance and Watters, 1971), now known as the Mawson Formation (Elliot and Hanson, 2001). Based on U/Pb and $^{40}Ar/^{39}Ar$ analysis of volcanic rocks in North Victoria Land, Musumeci et al. (2004) concluded that the pyroclastic event that led to the formation of the Prebble, Mawson, and Exposure Hill formations occurred between the Hettangian and lower Pliensbachian. However, given the sizable hiatus of Lower Jurassic rocks in South Victoria Land (Ribecai, 2007; Schöner et al., 2011), any fossils from the Mawson Formation in this area are likely to have been deposited later within this estimation.

The Mawson Formation is unconformably overlain by the Carapace Sandstone Formation, which is not present in all areas (Ribecai, 2007). However, the insect was collected on Carapace Nunatak where the formation is present and has been estimated to have been deposited during the upper Sinemurian to lower Pliensbachian (Ribecai, 2007). This means that the age estimation for the Mawson Formation in this area could lie within the later Hettangian to early late Sinemurian, making them of similar age to the English specimens.

Materials and methods

Collections of English material were examined from The Natural History Museum, London (NHMUK), the National Museum of

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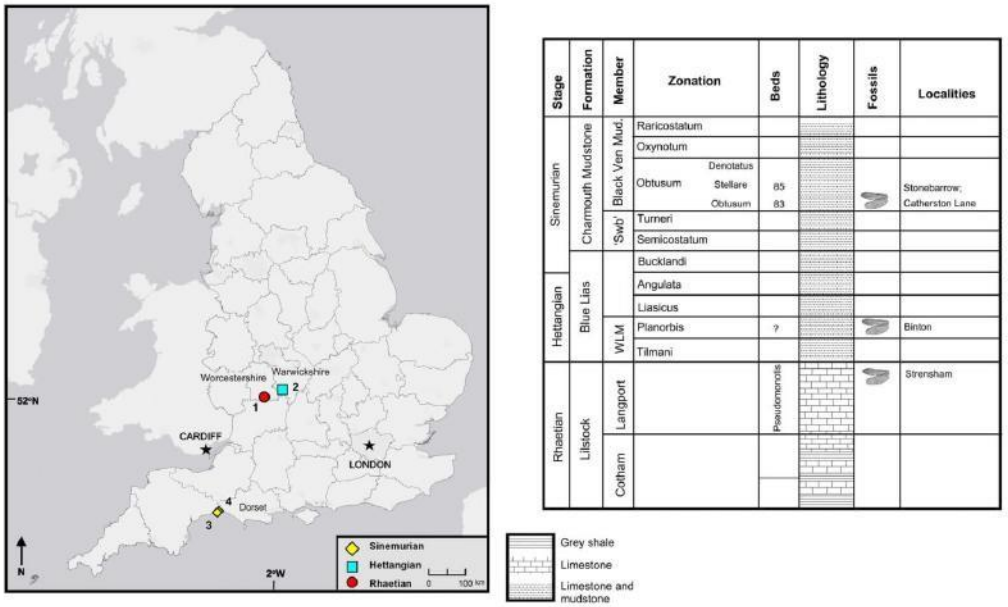

Figure 1. Locality map and stratigraphic chart for English specimens described herein. 1 = Strensham, Gloucestershire; 2 = Binton, Warwickshire; 3 = Stonebarrow, Dorset; 4 = Catherston Lane, Dorset; 'Swb' = 'shales-with-beef'; WLM = Wilmcote Limestone Member.

Wales, Cardiff (NMW), and the Oxford University Museum of Natural History (OUMNH). Photographs of the Antarctic specimen were examined from the National Museum of Natural History (United States National Museum), Smithsonian Institution, Washington, DC (USNM). All specimens from the English Midlands (Warwickshire and Worcestershire) were collected by the Rev. Peter Bellinger Brodie in the nineteenth century except for the OUMNH specimen, which was collected by the Rev. Frederick William Hope; all of the Dorset specimens were collected by James Frederick Jackson in the twentieth century except for the one collected from Catherston Lane, which was collected by a team of volunteers led by Kevin Page.

All specimens (except the holotype of *Caraphlebia antarctica*) were examined in person by the primary author and remotely via photographs by the co-author. Specimens were examined using the microscope equipment available at each museum and photographs were taken with a stand supporting a Nikon D3300 camera with AF-S Micro Nikkor 40-mm macrolens. Measurements were taken from photographs using the software package ImageJ (National Institutes of Health, ver. 1.51) and the scale of each image was calibrated using a standard ruler. Taxonomic figures were constructed in DrawPlus (Serif, version X8).

Venation nomenclature is based on the interpretations of Riek and Kukalová-Peck (1984), as modified by Nel et al. (1993) and Bechly (1996). Abbreviations are as follows: AA = anterior anal; AP = posterior anal; Arc = arculus; Ax = primary antenodal crossvein; Ax0 = first branch of primary antenodal crossvein; Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; C = costal vein; Cu = cubitus; CuA = anterior cubitus; CuA1 = distal branch of anterior cubitus; CuA2 = proximal branch of anterior cubitus; CuP = posterior cubitus; DC = discoidal cell; Ht = hypertriangle; IM = intercalary medial vein; IR = intercalary radial vein; IR1 = intercalary radial vein 1; IR2 = intercalary radial vein 2; MA = anterior median; MA1 = anterior branch of anterior median; MA2 = posterior branch of anterior median; MP = posterior median; N = nodus; 'O' = oblique vein; Pt = pterostigma; RA = anterior radius; RP = posterior radius; RP1 = first branch of posterior radius; RP2 = second branch of posterior radius; RP3/4 = third/fourth branch of posterior radius; ScP = posterior subcostal; T = triangle. The higher classification of fossil and extant Odonatoptera is based on the phylogenetic system of Bechly (1996, 2016).

Repositories and institutional abbreviations.—NHMUK, The Natural History Museum, London, UK; NMW, National Museum of Wales, Cardiff, UK; OUMNH, Oxford University Museum of Natural History, Oxford, UK; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Systematic paleontology

Order Odonata Fabricius, 1793
Suborder Epiprocta Lohmann, 1996
Superfamily Heterophlebioidea Needham, 1903
Family Liassophlebiidae Tillyard, 1925

Type genus.—*Liassophlebia* Tillyard, 1925.

Other genera.—*Ferganophlebia* Pritykina, 1970; *Grimmenopteron* Ansorge, 1996; *Bavarophlebia* Nel and Petrulevičius, 2005; *Rossiphlebia* new genus.

Emended diagnosis.—Discoidal cell basally closed in hindwing, sometimes with incomplete veinlet between 'hypertriangle' and discoidal triangle; discoidal cell open in forewing; subdiscoidal cell closed in both; subdiscoidal cell widened in forewing, with convex posterior margin; MP + CuA with very strong posterior curve in discoidal cell, so that subdiscoidal space is rather transverse; hindwings with unicellular anal loop enlarged; few, if any, antefurcal crossveins between RP and MA from arculus to midfork; no secondary antenodal crossveins between C and ScP (first row).

Remarks.—A nearly straight, long secondary vein in the postdiscoidal space slightly distal of the triangle is present in *Liassophlebia* and *Rossiphlebia* n. gen., but this vein is absent in *Grimmenopteron*, *Ferganophlebia*, and *Caraphlebia*.

Genus *Liassophlebia* Tillyard, 1925

Type species.—*Liassophlebia magnifica* Tillyard, 1925.

Emended diagnosis.—Cubito-anal area of hindwing large and broad, with 5 or 6 rows of cells between CuA and posterior wing margin; subdiscoidal space not divided into two large cells by anterior branch of AA that ends on CuA, but divided into small cells; wings very large.

Liassophlebia magnifica Tillyard, 1925

1925 *Liassophlebia magnifica* Tillyard, p. 15, pl. 1, fig. 3, pl. 2, fig. 4, text-figs. 3, 4.
1939 *Liassophlebia magnifica*; Handlirsch, p. 23.
1957 *Liassophlebia magnifica*; Asahina, p. 1, figs. 1, 3.
1962 *Liassophlebia magnifica*; Zeuner, p. 162, pl. 27, fig. 1.
1993 *Liassophlebia magnifica*; Nel et al., p. 139, fig. 107.
1995 *Liassophlebia magnifica*; Bechly, p. 16.
1996 *Liassophlebia magnifica*; Trueman, p. 69.
2003 *Liassophlebia magnifica*; Fleck et al., p. 56, 86.
2003 *Liassophlebia magnifica*; Rehn, p. 212.

Holotype.—NHMUK I.6648/I.10462 (Fig. 2), 'Insect limestone' of the Planorbis Chronozone (Lias Group, Blue Lias Formation, Wilmcote Limestone Member); Early Jurassic, Hettangian; Binton, Warwickshire. Female according to lack of anal angle and anal triangle.

Emended diagnosis.—Female hindwing, anal branch forks into subdiscoidal space forming distinct structure (also seen in *Liassophlebia pseudomagnifica*, but see below).

Remarks.—The specimen NHMUK I.11089 was also attributed to this species (Tillyard, 1925) but only a partial abdomen is preserved and so it is impossible to link it with any species described from wings. Zeuner (1962) also attributed NHMUK In.64000, In.59106, and In.49213 to this species, but the first is the holotype of *L. pseudomagnifica* (see below); the second is the holotype of *Hypsothemis fraseri* Whalley, 1985, and the last is a fragment of the anterior margin of a wing and is not identifiable at the species level.

Liassophlebia withersi Tillyard, 1925

1925 *Liassophlebia withersi* Tillyard, p. 17, pl. 3, fig. 8.
1939 *Liassophlebia Withersi*; Handlirsch, p. 23.
1962 *Liassophlebia withersi*; Zeuner, p. 164.
1993 *Liassophlebia withers*; Nel et al., p. 142, fig. 106.

Holotype.—NHMUK I.10697 (Fig. 3), 'Insect limestone' of the Pseudomonotis beds (Penarth Group, Lilstock Formation); Late Triassic, Rhaetian; Strensham, Worcestershire.

Diagnosis.—Similar to *Liassophlebia magnifica* but smaller (distance from arculus to distal acute angle of discoidal cell = 5.6 mm, compare to >6 mm in *L. magnifica*). Two anal cells, compared to three in *L. magnifica*.

Additional material.—NHMUK I.10528, from Strensham.

Remarks.—The two specimens discussed here are forewings, whereas the other described species are known mostly from hindwings, except for the partial forewing in *Liassophlebia magnifica*. The differences between this partial forewing and that of the holotype of *L. withersi* are few and better-preserved specimens could lead to the synonimization of this species with *L. magnifica*, or with one of the other species currently only described from hindwings. NHMUK I.10528 is a forewing originally attributed to *L. batheri* (which is herein considered nomen dubium, see below). Upon examination, it is clear that there are few differences between this specimen and the holotype of *L. withersi* except for the aberration in the anal vein of the holotype NHMUK I.10697 and an additional crossvein in the area immediately basal to the subdiscoidal cell. There is also a size difference; NHMUK I.10697 is 10.1 mm in width when measured level with the distal point of the discoidal triangle, and I.10528 is 11.3 mm. The distance from the distal point of the discoidal triangle to the point at which the arculus meets the radial vein in I.10697 is 5.1 mm and in I.10528 is 6.4 mm. Upon further material being described, they might be recognized as separate species, but there is little justification to split them with the evidence available.

Liassophlebia pseudomagnifica Whalley, 1985

1962 *Liassophlebia magnifica* Tillyard; Zeuner, p. 162, pl. 27, fig. 1.
1985 *Liassophlebia pseudomagnifica* Whalley, p. 120, fig. 5a, b.
1993 *Liassophlebia pseudomagnifica*; Nel et al., p. 139, figs. 104, 105.
2003 Liassophlebia pseudomagnifica; Fleck et al., p. 56.

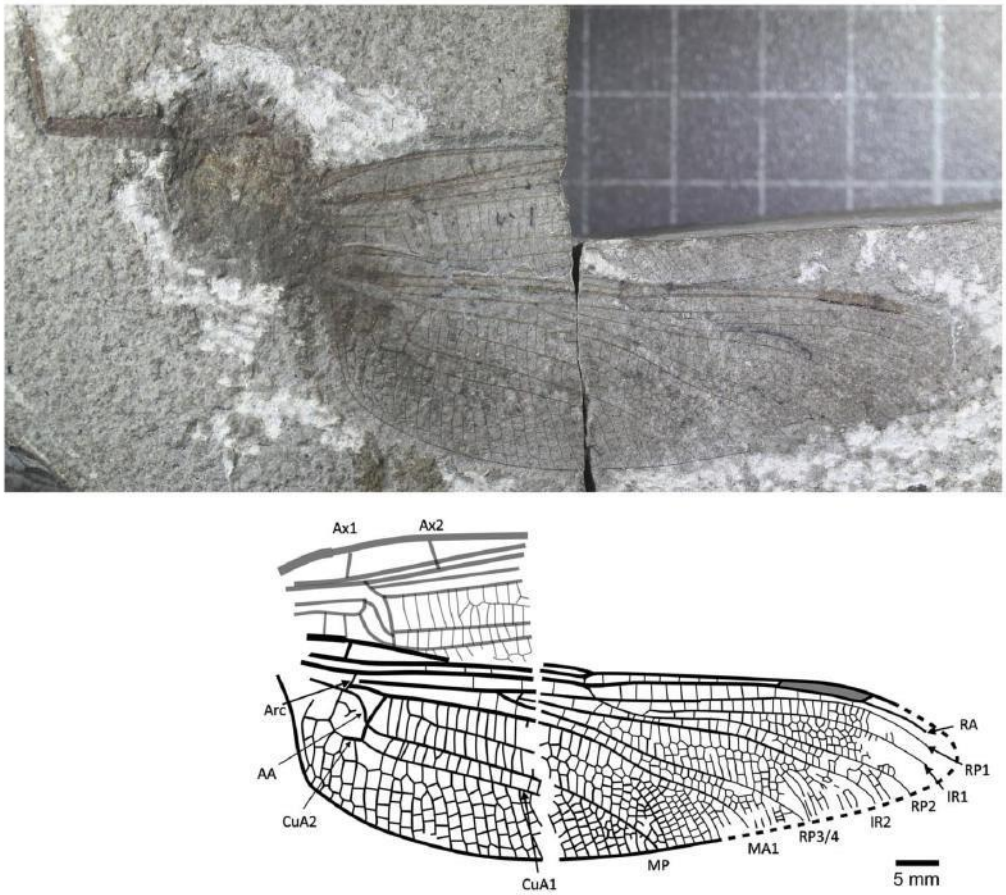

Figure 2. Holotype of *Liassophlebia magnifica* Tillyard, 1925 (NHMUK I.6648), Binton, Warwickshire (Hettangian), photograph and reconstruction. AA = anterior anal; Arc = arculus, Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; CuA1 = distal branch of anterior cubitus; CuA2 = proximal branch of anterior cubitus; IR1 = intercalary radial vein 1; IR2 = intercalary radial vein 2; MA1 = anterior branch of anterior median; MP = posterior median; RA = anterior radius; RP1 = first branch of posterior radius; RP2 = second branch of posterior radius; RP3/4 = third/fourth branch of posterior radius.

Holotype.—NHMUK In.64000 (Fig. 4), 'Flatstones' (bed 83) of the Obtusum Chronozone, Obtusum Subchronozone (Lias Group, Charmouth Mudstone Formation, Black Ven Mudstone Member); Early Jurassic, lower Sinemurian; Stonebarrow, Dorset.

Diagnosis.—Hindwing anal branch forking into subdiscoidal space similar to that seen in *Liassophlebia magnifica*; anal angle and triangle present.

Description.—See previous redescription by Nel et al. (1993).

Remarks.—This species was split from *Liassophlebia magnifica* based on a difference in the number of rows of cells between 'M and Cu' (Whalley, 1985), but it is clear from re-examination of the types that the numbers of rows are the same in the two specimens. Also, the peculiar shape of the anal vein in the subdiscoidal space is shared by *L. magnifica* and *L. pseudomagnifica*; this shape is not seen in any other species of liassophlebiid. The main differences between the two types of *L. magnifica* and *L. pseudomagnifica* are in the shape of the anal area, which is related to sexual dimorphism (presence of an anal angle and triangle in males), present in all Epiprocta (= 'Anisozygoptera' + Anisoptera). Another difference concerns the supplementary longitudinal vein in the basal part of the postdiscoidal area that begins three cells distal of the discoidal triangle in *L. magnifica* whereas it begins very close to it in *L. pseudomagnifica*. This difference could be due to intraspecific

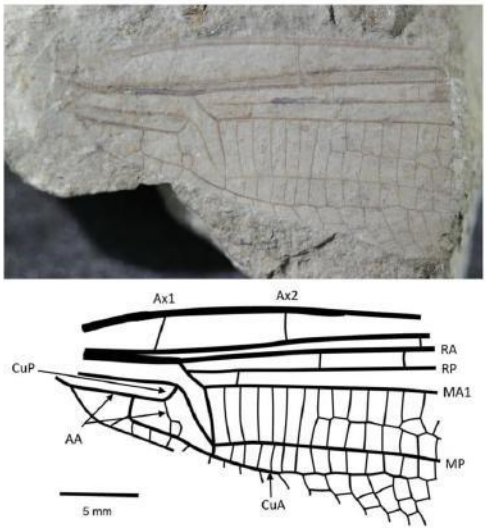

Figure 3. Holotype of *Liassophlebia withersi* Tillyard, 1925 (NHMUK I.10697), Strensham, Worcestershire (Rhaetian), photograph and reconstruction. AA = anterior anal; Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; CuA = anterior cubitus; CuP = posterior cubitus; MA1 = anterior branch of anterior median; MP = posterior median; RA = anterior radius; RP = posterior radius.

variation. There is no way to determine whether they belong to the same species until better preserved specimens are found.

Liassophlebia batheri Tillyard, 1925, nomen dubium

1925 *Liassophlebia batheri* Tillyard, p. 16, pl. 2, figs. 5, 6, pl. 3, fig. 7.
1939 *Liassophlebia batheri*; Handlirsch, p. 23.
1993 *Liassophlebia batheri*; Nel et al., p. 142.

Holotype.—NHMUK I.10434/10435 (Fig. 5), 'Insect limestone' of the Pseudomonotis beds (Penarth Group, Lilstock Formation); Late Triassic, Rhaetian; Strensham, Worcestershire.

Remarks.—The holotype of this species is referable to Liassophlebiidae based on similarity to the holotype of the type species but there are few other diagnostic characters to separate this specimen from other liassophlebiids from the UK. Additionally, there are no comparable characters between this specimen and the forewing specimen previously attributed to this species, so it is impossible to say whether they are the same species. NHMUK I.10528 was found to be very similar to *Liassophlebia withersi* and has been attributed to this species herein. Compared to *L. magnifica* (the type species of *Liassophlebia*), the pterostigma of I.10434 is similar; there are two or three fewer postnodal veins and several crossveins can be slightly more or less oblique, leading to an assumption that they are similar. However, the diagnostic characters of *L. magnifica* are not present and so it is impossible to accurately attribute this specimen to that, or any other, species. Given the lack of diagnostic characters and the removal of the forewing from the type series, it is clear that this species name should be considered nomen dubium.

Genus *Rossiphlebia* new genus

Type species.—*Liassophlebia jacksoni* Zeuner, 1962.

Diagnosis.—Male hindwing characters known. Strong anterior branch of AA ending on CuA and splitting subdiscoidal cell into two relatively large cells; cubital area wide (six or seven rows of cells); anal triangle split into two large cells in male; base of RP2 aligned with subnodus. Well-defined supplementary longitudinal vein in basal part of postdiscoidal area, beginning very close to discoidal triangle (also present in *Liassophlebia pseudomagnifica*).

Etymology.—Named for Dr. Andrew Ross, British palaeoentomologist and supervisor to the senior author.

Remarks.—This genus is very interesting because it seems to exhibit characters of both Liassophlebiidae and Heterophlebiidae. It is a liassophlebiid according to the rudimentary discoidal triangle and the presence of a well-defined supplementary longitudinal vein in the basal part of the postdiscoidal area, but the division of the subdiscoidal cell is similar to that of heterophlebiids, with a strong anterior branch of AA, but in male heterophlebiids, the anal triangle is split into three cells. The new genus is based on hindwing characters, thus it is difficult to compare with *Ferganophlebia* and *Grimmenopteron*, which are based on forewings only (Pritykina, 1970; Ansorge, 1996). Nevertheless, it differs from both (and from *Caraphlebia*) in the presence of a well-defined supplementary longitudinal vein in the basal part of the postdiscoidal area. It is not comparable to *Bavarophlebia*, which is based on a forewing, but in the latter, the base of RP2 is distinctly distal to the subnodus, whereas it is well aligned with it in *Rossiphlebia* n. gen.

Rossiphlebia jacksoni (Zeuner, 1962)

1962 *Liassophlebia jacksoni* Zeuner, p. 162, pl. 25, figs. 1, 2.
1985 *Liassophlebia jacksoni*; Whalley, p. 121, fig. 6.
1993 *Liassophlebia jacksoni*; Nel et al., p. 139, figs. 102, 103.

Holotype.—NHMUK In.53999, part and counterpart (Fig. 6), 'Flatstones' (bed 83) of the Obtusum Chronozone, Obtusum Subchronozone (Lias Group, Charmouth Mudstone Formation, Black Ven Mudstone Member); Early Jurassic, lower Sinemurian; Stonebarrow, Dorset.

Diagnosis.—Nine antenodal crossveins of second row; two or three rows of cells between MA1 and the supplementary longitudinal vein.

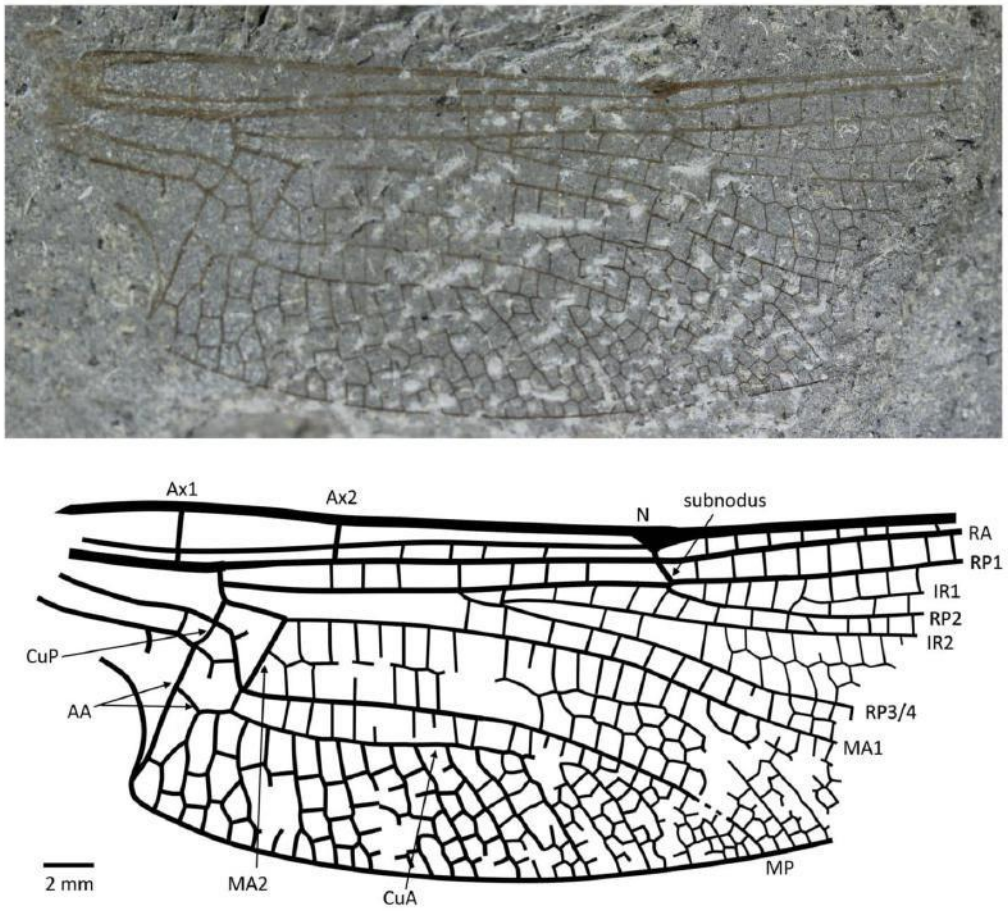

Figure 4. Holotype of *Liassophlebia pseudomagnifica* Whalley, 1985 (NHMUK I.64000); Stonebarrow, Dorset (Sinemurian); photograph and reconstruction. AA = anterior anal; Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; CuA = anterior cubitus; CuP = posterior cubitus; IR1 = intercalary radial vein 1; IR2 = intercalary radial vein 2; MA1 = anterior branch of anterior median; MA2 = posterior branch of anterior median; MP = posterior median; N = nodus; RA = anterior radius; RP1 = first branch of posterior radius; RP2 = second branch of posterior radius; RP3/4 = third/fourth branch of posterior radius.

Description.—See original description by Zeuner (1962).

Additional material.—NMW 91.14G.1, Catherston Lane.

Remarks.—This species is transferred to the new genus *Rossiphlebia* based on hindwing characters; no forewings are yet known.

Family Anglophlebiidae new family

Type genus.—*Anglophlebia* new genus.

Diagnosis.—As for the type species, by monotypy.

Etymology.—*Anglo*, the Latin prefix for England, and *phlebiidae*, a common suffix for Liassic dragonfly families.

Genus *Anglophlebia* new genus

Type species.—*Liassophlebia gigantea* Zeuner, 1962.

Diagnosis.—As for the type species.

Etymology.—*Anglo*, the Latin prefix for England, and *phlebia*, a common suffix for Liassic dragonfly genera.

Anglophlebia gigantea (Zeuner, 1962)

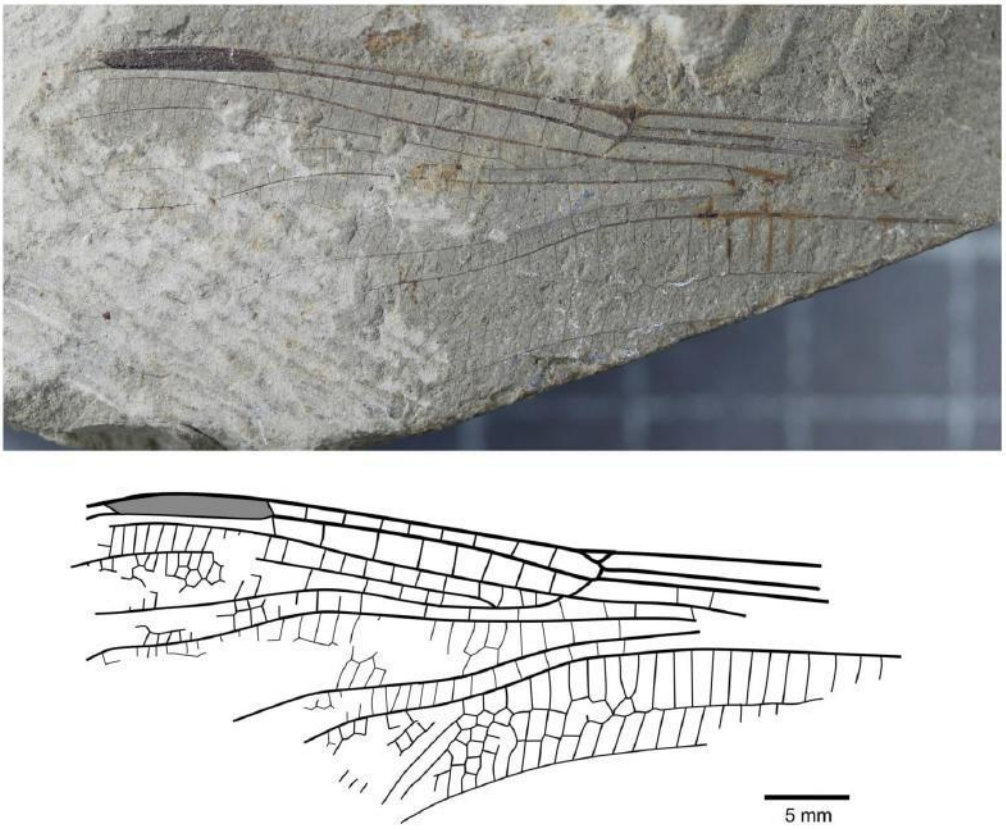

Figure 5. Holotype of *Liassophlebia batheri* Tillyard, 1925 (NHMUK I.10434), Strensham, Worcestershire (Rhaetian), photograph and reconstruction.

1962 *Liassophlebia gigantea* Zeuner, p. 163, pl. 27, fig. 2.
1985 *Liassophlebia gigantea*; Whalley, p. 122, fig. 7a, b.
1993 *Liassophlebia gigantea*; Nel et al., p. 139, fig. 108.

Holotype.—NHMUK In.51030, part and counterpart (Fig. 7), 'Flatstones' (bed 83) of the Obtusum Chronozone, Obtusum Subchronozone (Lias Group, Charmouth Mudstone Formation, Black Ven Mudstone Member); Early Jurassic, lower Sinemurian; Stonebarrow, Dorset.

Diagnosis.—Narrow wing with characters of both fore- and hindwings of the Liassophlebiidae: AA strongly curved posteriorly and straight (typical of forewings); posterior margin of subdiscoidal cell not convex and forking, with Cu appearing to extend toward posterior margin; subdiscoidal cell widened distally as in Liassophlebiidae; discoidal cell basally closed, with shape reminiscent of that in liassophlebiid hindwings; subdiscoidal space divided into three or four cells; at least six cells between subdiscoidal cell and wing base; cubital area very narrow (forewing character); intercalary medial vein beginning at first crossvein after distal margin of discoidal triangle (MA2) and stronger and smoother than that of liassophlebiids; also more cells in postdiscoidal area with possible second posterior intercalary vein.

Remarks.—This is a peculiar specimen because it seems to exhibit characters traditionally indicative of both fore- and hindwings. With the shape of the discoidal cell and the presence of the intercalary vein in the postdiscoidal area, it could be identified as a hindwing, as indeed it was by Zeuner (1962). However, in the counterpart, the cubito-anal area is better preserved and exhibits characters of a forewing (AA curving strongly posteriorly; shape of anal area; narrow cubital area) and of a hindwing (discoidal cell basally closed; shape of discoidal cell; intercalary vein in postdiscoidal area; subdiscoidal cell divided).

There are two possible hypotheses based on the evidence: (1) that we have a hindwing with a reduced cubito-anal area, as

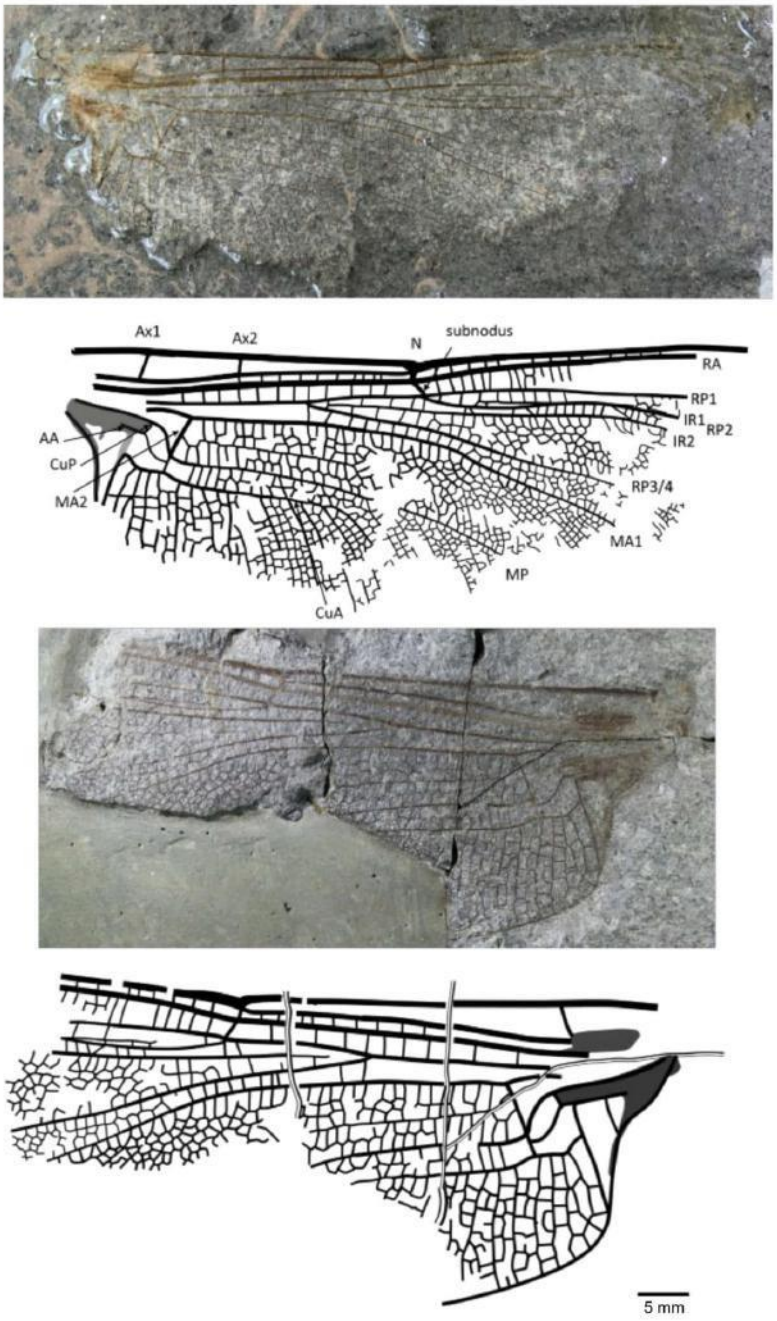

Figure 6. Holotype of *Rossiphlebia jacksoni* (Zeuner, 1962) (NHMUK In.53999, part and counterpart), Stonebarrow, Dorset (Sinemurian), photograph and reconstruction. AA = anterior anal; Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; CuA = anterior cubitus; CuP = posterior cubitus; IR1 = intercalary radial vein 1; IR2 = intercalary radial vein 2; MA1 = anterior branch of anterior median; MA2 = posterior branch of anterior median; MP = posterior median; N = nodus; RA = anterior radius; RP1 = first branch of posterior radius; RP2 = second branch of posterior radius; RP3/4 = third/fourth branch of posterior radius.

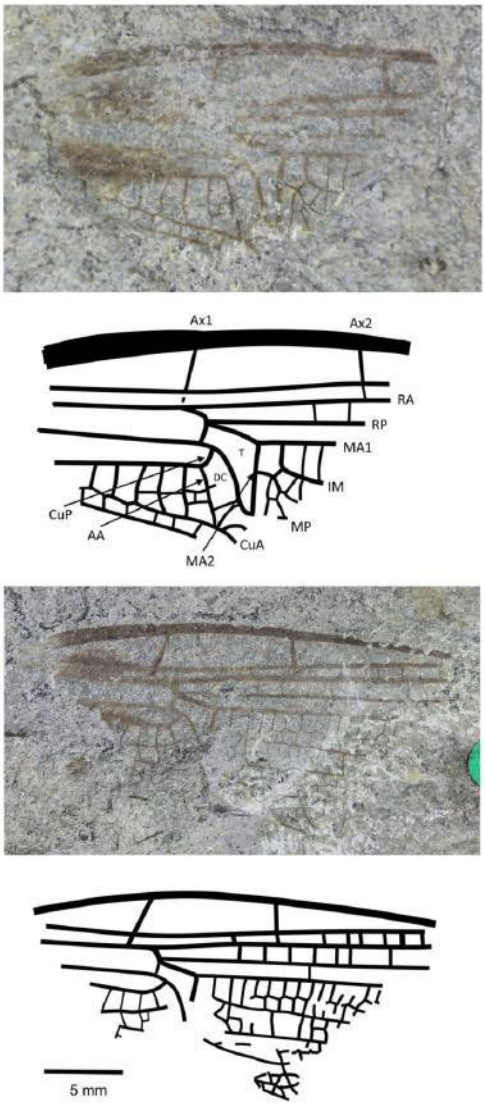

Figure 7. Holotype of *Anglophlebia gigantea* (Zeuner, 1962) (NHMUK In.51030 pt and cpt); Stonebarrow, Dorset (Sinemurian); photograph and reconstruction. AA = anterior anal; Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; CuA = anterior cubitus; CuP = posterior cubitus; DC = discoidal cell; IM = intercalary medial vein; MA1 = anterior branch of anterior median; MA2 = posterior branch of anterior median; MP = posterior median; RA = anterior radius; RP = posterior radius; T = triangle.

in some Campterophlebiidae (Nel et al., 2008), or (2) that we have a forewing with some hindwing characters (as in the Liassogomphidae Tillyard, 1935 and modern Anisoptera in which the discoidal cell is divided into a hypertriangle and a discoidal triangle in the forewings, compared to the Heterophlebiidae Handlirsch, 1906, in which this is only true in the hindwings). Either way, and although the specimen is only the basal fragment, it is unique among the British materials (checked at all known repositories of British Late Triassic–Early Jurassic material in the UK and the USA), the Liassic

material held in Paris at the Muséum National d'Histoire Naturelle (examined by AN), the Late Triassic–Early Jurassic Russian and Central Asian material (checked at the Paleontological Institute of the Russian Academy of Sciences in Moscow by RSK and Dmitry Vassilenko), and the Late Triassic–Early Jurassic material from China held at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (examined by RSK). The specimen does not fit with any family diagnosis already described and so we tentatively erect a new family for this species in the hope that further, better-preserved specimens will be found and described in the future.

Clade Isophlebioptera Bechly, 1996
Family Selenothemistidae Handlirsch, 1939

Genus *Caraphlebia* Carpenter, 1969

Type species.—*Caraphlebia antarctica* Carpenter, 1969.

Diagnosis.—A very well-defined CuA2 directed toward posterobasal side of hindwing.

Caraphlebia antarctica Carpenter, 1969

1969 *Caraphlebia antarctica* Carpenter, p. 419, fig. 1.
1993 *Caraphlebia antarctica*; Nel et al., p. 259, fig. 221.

Holotype.—USNM 165874, part and counterpart (Fig. 8), Ferrar Group, Mawson Formation; Early Jurassic, lower Lias (possibly Hettangian–Sinemurian); Carapace Nunatuk, South Victoria Land, Antarctica.

Diagnosis.—Hindwing CuA2 quite distinct, directed toward posterobasal margin of wing.

Description.—Primary antenodals present, Ax1 basal to arculus, Ax2 distal to it, arculus closer to Ax1 than to Ax2. Crossveins between RA and RP basal to expected position of subnodus; postnodal crossveins not visible. Pterostigma very long and narrow, but apparently distally incomplete. Postdiscoidal area not distally narrowed. Area between RP3/4 and IR2 apparently distally broadened. Oblique veins not preserved. Nodal structures very poorly preserved. RP2 and IR1 not discernible. Discoidal cell poorly preserved, but quite short and with distal side MA2 twice as long as basal side (without any trace of subdivision into hypertriangle and triangle, as figured by Carpenter, 1969). Subdiscoidal space broad, with posterior side (AA and CuA) convex. Basal part of CuA short, CuA2

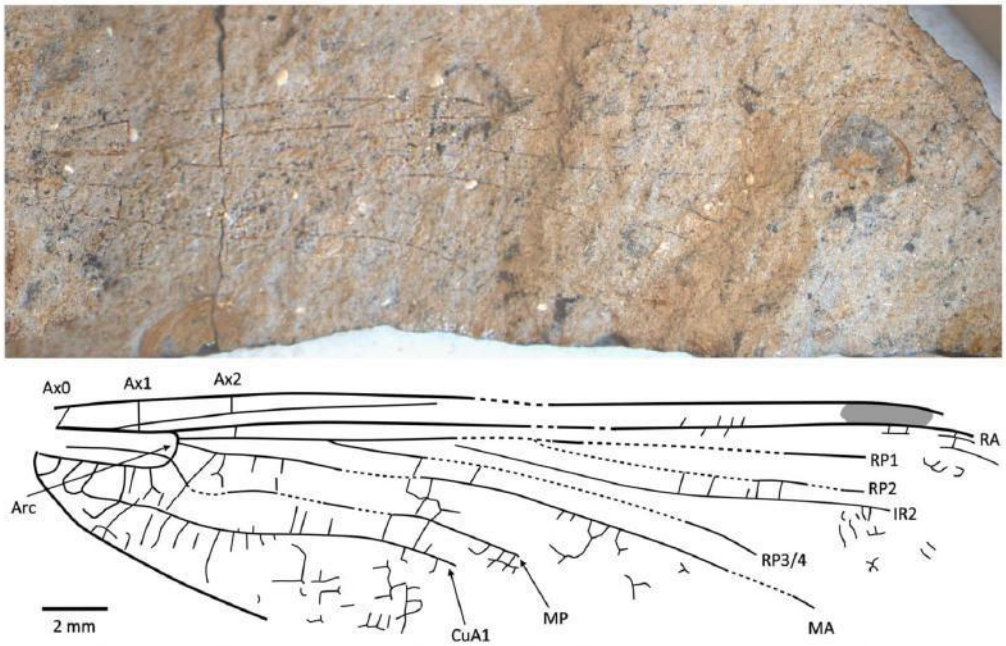

Figure 8. Holotype of *Caraphlebia antarctica* Carpenter, 1969 (USNM 165874), Carapace Nunatak (Hettangian to Sinemurian), photograph and reconstruction. Ax0 = first branch of primary antenodal crossvein; Ax1 = second branch of primary antenodal crossvein; Ax2 = third branch of primary antenodal crossvein; Arc = arculus; CuA1 = distal branch of anterior cubitus; IR2 = intercalary radial vein 2; MA = anterior median; MP = posterior median; RA = anterior radius; RP1 = first branch of posterior radius; RP2 = second branch of posterior radius; RP3/4 = third/fourth branch of posterior radius.

Figure 9. Holotype of '*Liassophlebia*' *clavigaster* Tillyard, 1925 (NHMUK I.10433), Strensham, Worcestershire (Rhaetian), photograph.

Figure 10. Holotype of '*Liassophlebia*' *hopei* (Brodie, 1845) (OUMNH J.55084); Strensham, Worcestershire (Rhaetian); photograph.

quite distinct, directed toward posterobasal margin of wing, with AA ending within it. Cubital area broad with ~5 or 6 rows of cells between CuA and posterior wing margin. Anal area broad with two rows of large cells. Anal margin rounded, without any angle; no anal triangle (female).

Remarks.—The original description and figure (Carpenter, 1969) shows an almost complete and supposedly well-preserved fossil. However, the type specimen (Fig. 8) is not as well-preserved with most of the apical half of the wing missing, although fortunately most of the major veins are preserved though slightly warped by the structure of the rock. The numerous secondary antenodal crossveins figured by Carpenter (1969, fig. 1) are not discernible. The pattern of the longitudinal veins, i.e., postdiscoidal space not narrowed and RP3/4 not parallel to IR2, corresponds to Liassophlebiidae and Selenothemistidae. However, the shape of the discoidal cell differs from that of liassophlebiids in that it is relatively short and without any trace of division into a hypertriangle and discoidal triangle. The probable absence of secondary antenodal crossveins and veins in the basal area between RA and RP also supports attribution to the Selenothemistidae. The quite well-defined CuA2, curved toward the posterobasal side of the wing, is very particular and probably is an autapomorphy of the genus.

Odonata incertae sedis, fam. indet.
'*Liassophlebia*' *clavigaster* Tillyard, 1925

1925 *Liassophlebia* (?) *clavigaster* Tillyard, p. 19, pl. 3, fig. 9, text-fig. 5.
1939 (Anisozygopteron) *clavigaster*; Handlirsch, p. 29.
1978 *Liassophlebia clavigaster*; Lindley, p. 344.
1993 *Liassophlebia* (?) *clavigaster*; Nel et al., p. 142, fig. 109.

Holotype.—NHMUK I.10433 (Fig. 9), 'Insect limestone' of the Pseudomonotis beds (Penarth Group, Lilstock Formation); Late Triassic, Rhaetian; Strensham, Worcestershire.

Remarks.—This specimen and the other identified as this species (NHMUK I.475) are known only from abdominal segments. Liassophlebiid higher taxonomy is based on wings so it is impossible to attribute this specimen to a genus or family. Therefore, we consider this species to be incertae sedis at those levels until a better-preserved specimen allows identification.

'*Liassophlebia*' *hopei* (Brodie, 1845)

1845 *Libellula hopei* Brodie, p. 71, pl. 10, fig. 3.
1892 *Libellula hopei*; Woodward, p. 195.
1879 *Libellula hopei*; Goss, p. 129.
1850 *Petalura liassina* (Strickland); Hagen, p. 359.
1850 *Heterophlebia hopei*; Selys-Longchamps and Hagen, p. 359 (footnote).
1906 (Anisozygopteron ?) *hopei*; Handlirsch, p. 470.
1939 (Anisozygopteron) *hopei*; Handlirsch, p. 29.
1925 *Liassophlebia* (?) *hopei*; Tillyard, p. 19.
1993 *Liassophlebia hopei*; Nel et al., p. 143.

Holotype.—OUMNH J.55084 a and b, 'Insect Limestone' of the Pseudomonotis beds (Penarth Group, Lilstock Formation); Rhaetian; Strensham, Worcestershire.

Remarks.—Same reasoning as for '*Liassophlebia*' *clavigaster*, above.

Discussion

Examination of the fossil material from the Late Triassic and Early Jurassic of England has led to several major changes to the taxonomy of Liassophlebiidae and changes to the diversity estimates of insects across the TJB. The new family Anglophlebiidae is tentatively erected for a specimen previously attributed to the liassophlebiid species *Liassophlebia gigantea* by Zeuner (1962). This specimen is only a fragment of a wing, and it is expected that future changes to the taxonomy of this family will be required as and when better-preserved specimens are found. However, the characters that are preserved are of sufficient uniqueness that it is important to draw attention to the specimen. This taxon is of particular interest because it appears to exhibit characters traditionally attributed to both fore- and hindwings, respectively narrow cubito-anal area vs. discoidal cell basally close and nearly divided into two parts by an incomplete crossvein.

Rossiphlebia n. gen. is erected for a species previously attributed to *Liassophlebia jacksoni* by Zeuner (1962). This species is clearly not attributable to *Liassophlebia* because the subdiscoidal space is subdivided into two large cells by a branch of AA. This genus is particularly interesting because it seems to exhibit characters of both Liassophlebiidae and Heterophlebiidae. As the taxonomy of these groups is revised, it is also important to consider the bigger picture and the effects of such findings on previous phylogenies (e.g., Nel et al., 1993). With the new characters described since 1993, the topography of a Jurassic Odonata phylogeny would probably look much different.

Two specimens—a forewing and a hindwing—were originally attributed to *Liassophlebia batheri* by Tillyard (1925).

Because these are isolated wings, it is impossible to ascertain whether they belong to the same species without a specimen that preserves both fore- and hindwings together. Moreover, the forewing was found to be very similar to the holotype of *L. withersi*, which is described from a forewing. The only real difference is an aberration in the anal area of the holotype and a size difference that is not sufficient to split them into separate species, so the forewing previously attributed to *L. batheri* is herein transferred to *L. withersi*. This leaves only the hindwing holotype of *L. batheri*, which is not of sufficient preservation for description and so the species is herein considered nomen dubium.

Two species—*Liassophlebia (?) clavigaster* and *L. (?) hopei*—were described from isolated abdominal segments. However, liassophlebiid higher taxonomy is described from isolated wings and there are yet to be any specimens described with both wing and abdomenal characters, so it is impossible to attribute isolated abdomens to the same taxa. The taxonomy of these specimens is not clear higher than family level because members of Stenophlebiidae also have apically widened abdomens similar to *L.* (?) *clavigaster*; it is therefore not yet possible to attribute these fossils to a precise higher group (e.g., Stenophlebiomorpha, Heterophlebioptera, etc.).

Taxonomic revision of historical collections is important because it increases our understanding of past diversity and allows us to better reconstruct palaeoentomofaunas. There are also implications for our understanding of insect phylogenies because several of the species described herein exhibit characters from traditionally separate families. The current revision did not however have much of an effect on our understanding of the impact of the ETE on insect diversity. We consider *L. batheri* to be nomen dubium and we transferred the other specimen identified as this species to *L. withersi*; this reduced the species richness of insects in the Rhaetian by one (*L. batheri*) but did not affect the ranges of other species or the genus. There were no taxonomic changes to *L. magnifica* and no further specimens were found, so there were no changes to the range of this species and so it still seems to have originated in the Hettangian following the ETE. Selenothemistidae was previously only known from the Toarcian of Germany (Handlirsch, 1939) so the confirmation of *Caraphlebia* in this family increases the range of the family back to the Hettangian or Sinemurian, indicating that the family originated closer to the TJB and prior to the early Toarcian mass extinction. *Rossiphlebia* n. gen. and Anglophlebiidae n. fam. are newly described but are only known from the Sinemurian. Their description increases the diversity of insects in the Sinemurian but does not affect the range of Liassophlebiidae or *Liassophlebia* across the TJB.

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Earwigs (Dermaptera) from the Mesozoic of England and Australia, described from isolated tegmina, including the first species to be named from the Triassic

Richard S. Kelly,[1,2] Andrew J. Ross,[2,4] and Edmund A. Jarzembowski[3,4]

[1] School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Street, Bristol BS8 1TH, UK.
[2] Department of Natural Sciences, National Museum of Scotland, Chambers Street, Edinburgh EH1 1JF, UK.
[3] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China.
[4] Department of Earth Sciences, Natural History Museum, London SW7 5BD, UK.

ABSTRACT: Dermaptera (earwigs) are described from the Triassic of Australia and England, and from the Jurassic and Cretaceous of England. *Phanerogramma heeri* (Giebel) is transferred from Coleoptera and it and *Brevicula gradus* Whalley are re-described. Seven new taxa are named based on tegmina: *Phanerogramma australis* sp. nov. and *P. dunstani* sp. nov. from the Late Triassic of Australia; *P. gouldsbroughi* sp. nov. from the Triassic/Jurassic of England; *Brevicula maculata* sp. nov. and *Trivenapteron moorei* gen. *et* sp. nov. from the Early Jurassic of England; and *Dimapteron corami* gen *et* sp. nov. and *Valdopteron woodi* gen. *et* sp. nov. from the Early Cretaceous of England. *Phanerogramma*, *Dimapteron* and *Valdopteron* are tentatively placed in the family Dermapteridae, and *Trivenapteron* is *incertae sedis*. Most of the specimens of *Phanerogramma heeri* are from the Brodie Collection and labelled 'Lower Lias'; however, some were collected from the underlying Penarth Group, thus this species spans the Triassic/Jurassic boundary. The palaeobiogeography of the Late Triassic and Early Jurassic of England is discussed.

KEY WORDS: Archidermaptera, palaeobiogeography, palaeoentomology, Polyneoptera, taxonomy/systematics.

The earwigs (Insecta: Dermaptera) form a relatively small, easily recognisable order. They are elongate and dorsoventrally flattened with short leathery forewings (tegmina), which cover only the most anterior part of the abdomen. They look superficially similar to staphylinid beetles, except that earwigs have specialised cerci which are usually modified into forceps. These are used for defence, to aid in copulation, to unfurl and fold their fan-like hindwings and to capture prey in predatory species. The hindwings are also distinctive, with much of the venation in the remigium reduced and a large, well defined anal region with distinctive creases for the unique folding pattern of their wings. The head is triangular and prognathous. Compound eyes are well developed and ocelli are always missing in modern species; however, some fossil species have been found with three ocelli. The mouthparts are mandibular and are similar to those of orthopterans. The pronotum is rectangular with rounded corners and is distinctive enough between species to have its length to width ratio used in identification.

There are approximately 1,900 living species of earwig (Grimaldi & Engel 2005), although they are rare in the fossil record, with 86 described species. Sixty-six extinct species and additional unnamed fossil specimens were listed by Wappler *et al.* (2005), and an additional 23 extinct species were described or transferred from other orders by Zhang (1997), Haas (2007), Chatzimanolis & Engel (2010), Zhao *et al.* (2010a, b, 2011), Engel (2011), Engel *et al.* (2011, 2015, 2016), Perrichot *et al.* (2011), Nel *et al.* (2012), Ross & Engel (2013), Engel & Grimaldi (2014), Engel & Perrichot (2014), Yang *et al.* (2015) and Xing *et al.* (2016).

Their stratigraphic range largely depends on the placement of the Protelytroptera which are known from the early Permian. Originally, these were considered as a separate order preceding the Dermaptera (Tillyard 1931; Carpenter 1992). Shcherbakov (2002) placed the Protelytroptera and the Dermaptera, based on the presence of earwig-style wing-folding and metascutal setose ridges, in the order Forficulida with two suborders: Protelytrina and Forficulina, constituting the original Protelytroptera and Dermaptera respectively. Whilst some authors recognise four suborders – Hemimerina, Arixeniina, Forficulina and Archidermaptera – (for example Haas 1995), Engel & Haas (2007) undertook an extensive review of higher earwig taxonomy, although referencing Shcherbakov's suggestion, and regarded Protelytroptera as a separate order. Within the Dermaptera, their classification includes the extinct suborders Archidermaptera and Eodermaptera, with Neodermaptera as the only extant suborder. This classification has been followed by others (e.g., Gullan & Cranston 2010; Zhao *et al.* 2010b; Perrichot *et al.* 2011; Nel *et al.* 2012; Kocarek *et al.* 2013) and is followed herein.

The earliest recorded Dermaptera are tegmina from the Late Triassic of England, Australia and Kyrgyzstan (Jarzembowski 1999; Wappler *et al.* 2005; Shcherbakov 2008), although it has been suggested that the preservation of the Triassic specimens is too poor and that earwigs originated in the early Mesozoic of Asia (Zhao *et al.* 2010b). Only two species have been described from the Early Jurassic: *Brevicula gradus* Whalley, 1985 from the Lower Lias (Sinemurian) of England is often cited as the oldest described fossil dermapteran; however, there is another

species, *Baseopsis forficulina* Heer, 1865, from the Lower Lias of Switzerland, which Wappler *et al.* (2005) considered to be Hettangian in age and therefore older. Certainly, from the figure in Heer (1865, plate 7, fig. 5), the shape of the tegmina is consistent with Dermaptera; however, the specimen requires re-examination to confirm it is a dermapteran. Most of the Heer collection is held at the Swiss Federal Institute of Technology (ETZ), but the specimen could not be located for examination (Andreas Müller, pers. comm. 2016). A further species, *B. sibirica* Brauer *et al.*, 1889, was named from the Toarcian of Russia. This specimen is probably held at the Geological Museum of the Academy of Sciences in Moscow (PIN), with the rest of the Czekanowski collection. Wappler *et al.* (2005) list 18 further species from the Middle and Late Jurassic of China, Germany, Kazakhstan and Russia, and four more Middle Jurassic species from China were described by Zhao *et al.* (2010a, b, 2011). Given that these early Dermaptera fossils have small tegmina, Haas (2003) hypothesised that they were able to fold their hindwings like modern earwigs, and certainly the species from China described by Zhang (2002) have the remnants of hindwings, which appears to support this theory.

Herein, we formally describe the specimens of Dermaptera from the Late Triassic of Australia and England (mentioned above), along with additional material from the Jurassic and Cretaceous of England. The material is largely based on isolated tegmina which have not previously been used for dermapteran taxonomy. Many of the specimens were languishing in the collections at the Natural History Museum, London (NHM), but were not recognised as Dermaptera. It was not until a visit to the museum from Dr Dima Shcherbakov (Palaeontological Institute, Moscow) in the 1990s that their true identity was realised, when he informed AJR as to what they were.

1. Materials and methods

Two specimens labelled "Insect fragment" are in the Dunstan Collection, purchased by the NHM in 1935, of Late Triassic insects from Denmark Hill, Ipswich, Queensland, Australia, but which are clearly dermapteran tegmina. They are the oldest undoubted Dermaptera in the world.

Most of the English specimens are from the Brodie collection, purchased by the NHM in 1898. Although most of the specimens have locality data, they are labelled 'Lower Lias'. Thus, it could be assumed that they are Early Jurassic; however, at some of these localities the insect-bearing horizons occur within the Penarth Group of Late Triassic age. Details on the localities and probable ages are provided below. Previously, the position of the Triassic/Jurassic (Tr/J) boundary was unclear, but the establishment of the GSSP for the Tr/J boundary at Kuhjoch (Karwendel mountains, Tyrol, Austria) (Hillebrandt *et al.* 2013) has allowed the standardisation of the boundary in the UK. The boundary is set at the base of the *Psiloceras tilmani* Zone and, although the characteristic species of this zone, *P. tilmani*, is not present in English deposits, the zone has been correlated with the English Pre-planorbis beds (Page 2010; Cope 2012).

Thirty specimens were studied from the Penarth Group (Rhaetian) and Lias Group (Hettangian to Toarcian) of England. Nineteen of these were collected by Brodie, two by Jackson and one by Sole and are held at the NHM (specimens pre-fixed NHMUK); of these, five were too poorly preserved to be identified. One specimen was collected by Hope and is held at the Oxford University Museum of Natural History (OUMNH), one was collected by Moore and is held at the Somerset Heritage Centre for The Museum of Somerset, Taunton (TTNCM) and three were collected by Rob Coram and were donated to the NHM for the current study. Two further specimens are held in the USA, one Brodie specimen is held at Harvard University's Museum of Comparative Zoology (MCZ), which was found using the iDigBio online catalogue, and the other was collected by Lacoe and is held at the Smithsonian Institute in Washington (USNM). From close study of these specimens, it is clear that at least four species are present, three of which are described here as new.

In addition, there are five more specimens from the Cretaceous of England: two from the Durlston Formation (Berriasian) of Dorset, and three from the Upper Weald Clay Formation (Barremian) of Surrey. They represent two new genera and species. The vein terminology of Vishniakova (1980) is generally followed here, except that it is often not possible to distinguish R from Rs or CuA from CuP, in which case only R and Cu (undifferentiated) are recognised.

The specimens were studied using light microscopes (Leica models as available at the different institutes) and photographed using a Nikon D3300 with AF-S Micro Nikkor 40 mm macro lens attached. For specimens with similar morphology, but with a range of sizes, a bivariate plot using tegminal length and width was plotted in the stats program R (R Development Core Team 2016) and was examined for evidence of specimens grouped by size. A formal cluster analysis was not possible, due to small sample sizes and a limited number of variables for measurement.

2. Localities and ages

Figure 1 is a map of the Dermaptera localities in central and south-west England. Figure 2 is a general stratigraphic column of the localities described below and Figure 3 is a more detailed stratigraphic log of the probable Dermaptera horizons from near the Tr/J boundary.

Denmark Hill, Australia (Carnian). Two specimens in the Dunstan collection are from Denmark Hill, Ipswich, Queensland, Australia. The Denmark Hill Insect Bed occurs in the Blackstone Formation of the Ipswich Coal Measures Group of Carnian age (Webb 1982).

Prior's Norton, Gloucestershire National Grid Reference [SO 855 241] (Rhaetian). Brodie labelled these specimens as 'Norton'. The exact horizons of Brodie's insect limestone at this locality were never published and Brodie did not mention the locality in his book (Brodie 1845). The section was described by Richardson (1903, p. 141), which includes a series of dark shales (Rhaetic black shales) overlying the Rhaetic Bone Bed and containing the zonal bivalve *Avicula contorta*. These shales are similar to the beds of early Rhaetian age described at Charfield [ST 723 919] (Richardson 1904). Although the exact horizon cannot be gleaned from the available literature, it is clear that insect fossils from this locality are Rhaetian, probably from the Westbury Formation.

Wainlode Cliff, Gloucestershire [SO 845 257] (Rhaetian). This section is found approximately 5.5 km north of Gloucester and approximately 3 km southwest of Apperley. The section can be found at a westerly bend in the River Severn near the Red Lion Inn. There is decent exposure of the lower Penarth Group, with the top of the section obscured (Worssam *et al.* 1989). The stratigraphy of the section is similar to that at Aust Cliff [ST 563 888], with the Westbury Formation and then the Cotham Member of the Lilstock Formation at the top. The insects are found in the Cotham member and several collectors, including Brodie and EAJ, have found other types of insects at Wainlode.

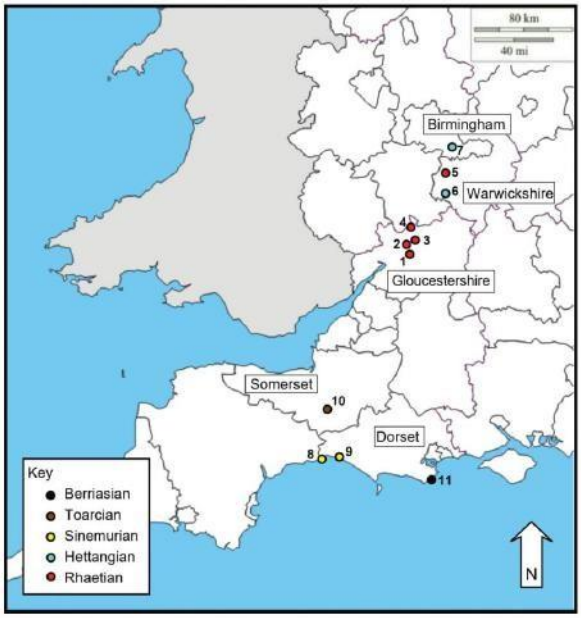

Figure 1 Localities of Mesozoic earwig-bearing horizons in central and southern England. Rhaetian: 1 = Prior's Norton; 2 = Wainlode Cliff; 3 = Apperley; 4 = Forthampton; 5 = Brown's Wood. Hettangian: 6 = Binton; 7 = Copt Heath. Sinemurian: 8 = Monmouth Beach; 9 = Black Ven. Toarcian: 10 = Ilminster. Berriasian: 11 = Durlston Bay.

Epoch	Stage	Localities
Lower Cretaceous	Albian	
	Aptian	
	Barremian	Smokejacks Brickworks, Surrey.
	Hauterivian	
	Valanginian	
	Berriasian	Durlston Bay, Dorset.
Upper Jurassic	Tithonian	
	Kimmeridgian	
	Oxfordian	
Middle Jurassic	Callovian	
	Bathonian	
	Bajocian	
	Aalenian	
Lower Jurassic	Toarcian	Ilminster, Somerset.
	Pliensbachian	
	Sinemurian	Monmouth Beach and Black Ven, Dorset.
	Hettangian	Binton, Warwickshire and Copt Heath, Birmingham
Upper Triassic	Rhaetian	Prior's Norton, Wainlode Cliff, Apperley and Forthampton, Gloucestershire; Browns Wood, Warwickshire.
	Norian	
	Carnian	Denmark Hill, Australia

Figure 2 Stratigraphy of all earwig-bearing localities described in this study.

Apperley, Gloucestershire [SO 862 284] (Rhaetian). Brodie (1845) describes the insect limestone at Apperley as being found in a small quarry on Grey Hill where Worssam *et al.* (1989) described a Penarth Group outcrop. The quarry described by Brodie was overgrown by the time Richardson (1903, p. 140) described a section there. Richardson considered Brodie's 'Insect Limestone' to be the Pseudomonotis bed, which he thought to be an attenuated form of the Langport Member or White Lias in Gloucestershire, found at the top of the Penarth Group.

Brown's Wood, Warwickshire [SP 116 641] (Rhaetian). The stratigraphy of this locality has been described as being similar to Shelfield [SP 123 624] and Wainlode Cliff (Brodie 1863, 1865). The insect bed at Brown's Wood was located by Brodie (1865), overlying the Estheria and Pecten beds, which are old terms for the Cotham Member and the Westbury Formation, respectively. Swift (1995) studied the occurrence of the White Lias throughout Britain. The White Lias is absent in Gloucestershire and is replaced by the Pseudomonotis bed;

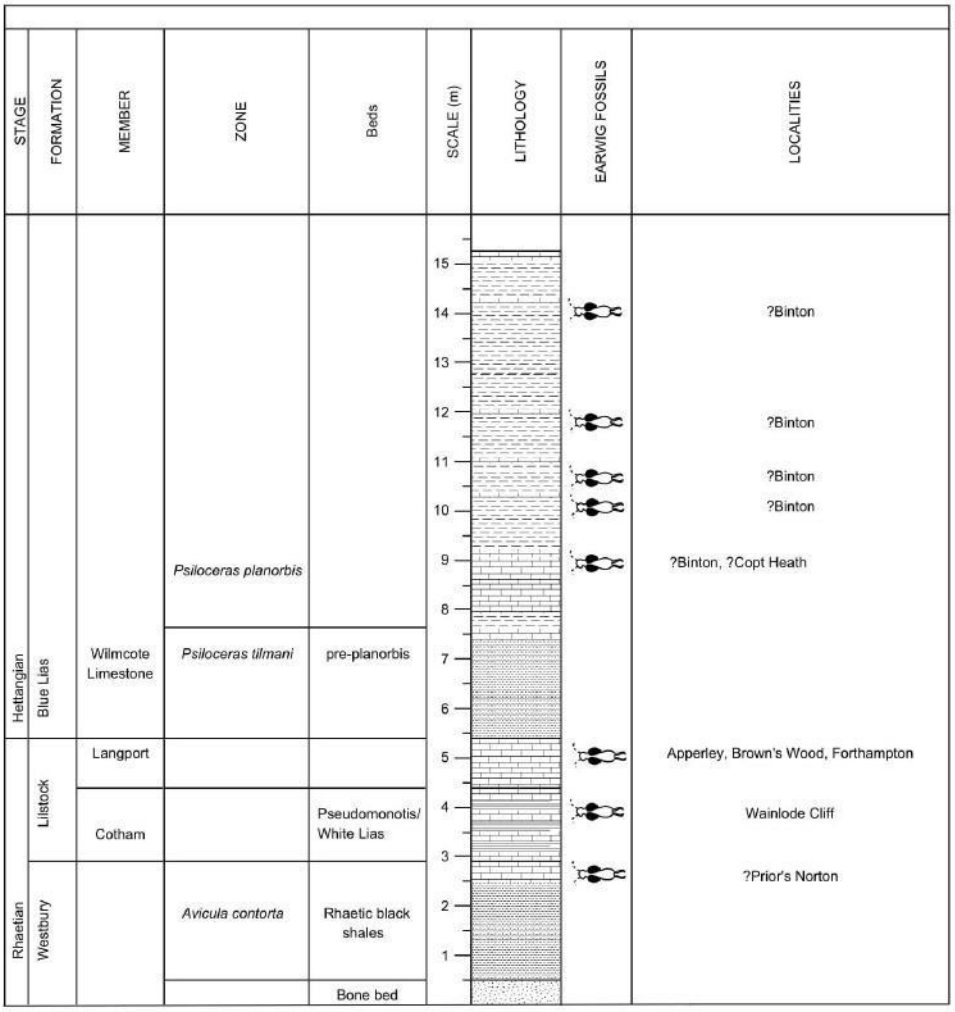

Figure 3 Stratigraphic position of earwig-bearing horizons near the Tr/J boundary in England. Localities are accurately dated to stage and several higher resolution horizons are estimated (indicated by ?). Horizons labelled "?Binton" are all horizons from which insects have been collected, but the precise horizon(s) from which earwigs were collected is/are unknown. Image made in SedLog 3.1 (Zervas *et al.* 2009).

but in Warwickshire, the White Lias is present, so the insect-bearing bed lying above the Cotham Member is probably in the White Lias (Langport Member).

Forthampton, Gloucestershire [SO 857 324] (Rhaetian). Popov *et al.* (1994) stated that the section at Forthampton correlates with the Pseudomonotis bed. Brodie (1845, p.66) described the section at Forthampton, and only a relatively thin bed of brown laminated shale (~30 cm) separates the Ostrea beds of the Pre-planorbis beds from the underlying insect limestone.

Binton, Warwickshire [SP 142 536] (Hettangian). Brodie (1845) indicated that there were several localities and horizons that yielded insects at Binton. A section for one of them, Osborne's Pit, was published by Brodie (1868), but it is uncertain exactly where this site was (Williams *et al.* 1974, p.39). The insect limestones at Binton all lie above the Pre-planorbis beds (Ostrea beds), so are within the *Psiloceras planorbis* Zone (Richardson 1912). Wright (1860) details the stratigraphy at Binton and indicates that insects are found in five beds above the Pre-planorbis beds: bed 15, 'Bottom rock', 0.98 m above; bed 13, 'paving stone', 1.3 m above, found along with the fish *Pholidophorus stricklandi*; bed 11, 'Ribs', a greyish limestone 1.5 m above; bed 5, 'top liveries', 2.5 m above; and bed 3, 'top liveries', 4.6 m above, in argillaceous limestone within the *Caloceras johnstoni* subzone. The most fossiliferous was the 'bottom rock': "more insects were found here than in all the other beds collectively". Unfortunately, it is not known from exactly which horizons the dermapteran fossils came.

Copt Heath, near Knowle, Birmingham [SP 175 780] (Hettangian). The insect limestone at this locality was said to lie in detached pieces scattered throughout the field, but

with no section exposed (Brodie 1874). Also recorded were the 'firestones and guinea-bed', which belong to the Wilmcote Limestone Member of the Blue Lias Formation (Old *et al.* 1991). Brodie also recorded the presence of the zonal ammonite *Psiloceras planorbis* in these blocks of 'firestones and guinea-bed', which would suggest a Hettangian age for the insects.

Morton Bagot, Warwickshire [SP 112 646] (Rhaetian). This locality is noted as a separate locality on some of Brodie's labels in NHMUK, but may also be referred to as "Brown's Wood, Moreton Bagot". In Matley (1912, p. 259, fig. 259), Morton Bagot is labelled as Brown's Wood, even though it is referred to as Morton Bagot in the text. As there is almost no further literature referring to Morton Bagot as a separate locality, we consider this to refer to the same locality as Brown's Wood, 1 km south of the village of Morton Bagot.

Monmouth Beach, Dorset [SY 329 911] (Sinemurian). Isolated tegmina have been found here in 'Birchi nodules' (bottom of Bed 75, *Caenisites turneri* Zone) of the Charmouth Mudstone Formation: Black Ven Mudstone Member (see Ross 2010).

Black Ven, Dorset [SY 355 930] (Sinemurian). Complete dermapteran specimens have been collected from the 'Birchi nodules' (bottom of Bed 75, *Caenisites turneri* Zone), 'Flat-stones' and 'Woodstones' (Bed 83, *Asteroceras obtusum* Zone) of the Charmouth Mudstone Formation: Black Ven Mudstone Member (see Ross 2010).

Strawberry Bank, Ilminster, Somerset [ST 361148] (Toarcian). Charles Moore collected many insects from this site in Ilminster. Although he produced a log of this site, he did not mark where the insects were found; however, Matt Williams (pers. comm. 2015) considers they probably came from his 'saurian and fish zone' thus from the *Harpoceras falciferum* Zone of the Upper Lias (Williams *et al.* 2015).

Durlston Bay, Dorset [SZ 035 780] (Berriasian). Two specimens were found here. The first was collected by Mrs Burnett and is only labelled 'Swanage'. The second, belonging to the same species, was collected by Rob Coram from the Corbula Beds within the Durlston Formation: Stair Hole Member (Coram & Jepson 2012). The 'Swanage' specimen is preserved in a blue/grey micrite, which is typical of Bed DB175 of the Corbula Beds (see Rasnitsyn *et al.* 1998).

Smokejacks Brickworks, Surrey [TQ 113 373] (Barremian). One specimen was found in the Upper Weald Clay Formation at this site, on the north face in a very fossiliferous large phosphatic lens (2 x 1.5 x 0.1 m), collected in 1996. The top of the lens lay 70 cm below the top of the lowest bed of dark grey shale that yields the plant *Bevhalstia* (see Novokshonov *et al.* 2016). Dislodged sideritic concretions in the northeast face have yielded two further specimens, correlated with the *Bevhalstia*l shale beds in the north face.

3. Systematic palaeontology

Order Dermaptera de Geer, 1773
Suborder Archidermaptera Bei-Bienko, 1936
Superfamily Protodiplatyoidea Martynov, 1925
?Family Dermapteridae Vishniakova, 1980

Type genus. *Dermapteron* Martynov, 1925 nom. transl. Vishniakova, 1980.

Remarks. The family Dermapteridae was originally named as the subfamily Dermapterinae Vishniakova, 1980 and was elevated to family status by Engel (2003) without discussion (the family Sinopalaeodermatidae Zhang, 2002 was included as a junior synonym by Engel & Haas (2007) without discussion). The subfamily name was Latinised based on Dermatopteron Martynov, 1925 originally proposed as a collective group. Nel *et al.* (2012) restored the Greek spelling, but as this is an unnecessary change, we have followed Vishniakova. The question mark in '?Family Dermapteridae Vishniakova 1980' above is used to denote uncertainty as to the placement of the genera described below, not to question the authority of the family name.

Genus *Phanerogramma* Cockerell, 1915

Emended diagnosis. Tegmina not truncated, tuberculate, with evenly curved anterior margin. M and Cu have a common origin, Cu simple.

Type species. *P. heeri* (Giebel 1856).

Remarks. Brodie (1845, p1. 8, figs 15, 17, 18) figured three specimens from the 'Lower Lias' of England and considered them to "either be the hemelytron of some new genus of Homoptera, or some curiously striated elytron of a beetle" (Brodie 1845, p. 128). Giebel (1856) named two of Brodie's figured specimens as two new species of the extant orthopteran genus *Akicera*: *A. heeri* and *A. frauenfeldi*. In Brodie (1845, p. 101), a mistake led to one of the figures (fig. 17) being listed as 'Blattidae?' from Wainlode and Strensham; however, this should probably have been a reference to figure 13 instead, which is a partial blattodean (cockroach) wing. This led to Scudder (1891, p. 104) incorrectly citing *A. heeri* as being from these localities. Cockerell (1915) synonymised the two species and placed them in the new genus *Phanerogramma* in the beetle (Coleoptera) family Tenebrionidae, where the taxon has languished ever since. *P. heeri* became the senior synonym over *P. frauenfeldi*.

Of the three specimens figured by Brodie, two are clearly labelled; however, the third cannot be found. Unfortunately, the missing specimen is the holotype of *Phanerogramma heeri*. A thorough search through the 19 Dermaptera tegmina in the Brodie collection at the NHM has not established if any one of them could be the missing type. They came from several different localities, but unfortunately the location of the type is not known. Either this specimen is present but unlabelled and impossible to recognise, or it is missing. For this reason, a neotype is required for *Phanerogramma heeri* from Brodie's collection.

All the tegmina are characteristic in having a distinctive tuberculate ornament. *Dermapteron incertus* (nom. correct. pro *incerta* Martynov, 1925) (Dermapteridae) and *Asiodiplatys speciosus* Vishniakova, 1980 (Protodiplatyidae) both have a granular ornament within the Protodiplatyoidea; however, *Dermapteron* has a richer venation (see Vishniakova 1980). *Phanerogramma* is also similar to *Sinopalaeodermata neimonggolensis* Zhang, 2002 and *Palaeodermapteron dicranum* Zhao *et al.*, 2011, both within the Dermapteridae (*sensu* Engel & Haas 2007). *Phanerogramma* differs from *Dermapteron*, *Sinopalaeodermata* and *Palaeodermapteron* in having a more evenly curved anterior margin and Cu is simple not forked. *Phanerogramma* certainly belongs to the Protodiplatyoidea, but given that the body morphology is not known, it is only tentatively placed within the family Dermapteridae based on the venation.

The Australian specimens are clearly similar and can be placed in the same genus. Examination of the bivariate plot of the more complete English and Australian specimens resulted in a central group with two satellites (Fig. 4). The central group can be regarded as one species and includes the specimen originally named *P. frauenfeldi;* thus, a neotype of *P. heeri* was chosen from this group. The two satellites are

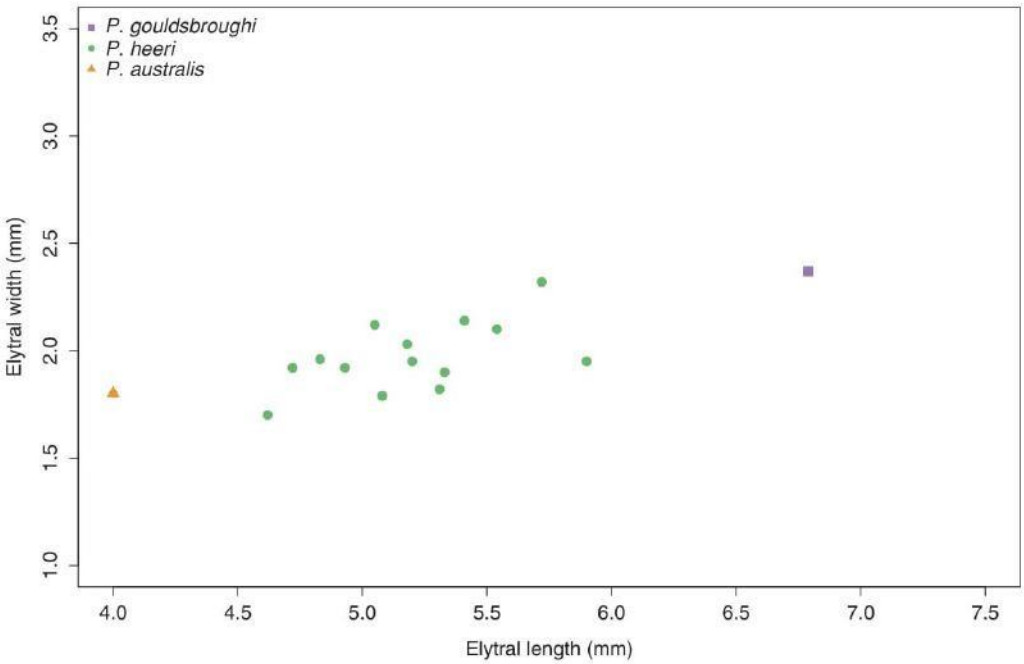

Figure 4 Relationship between length and width of tegmina. Three possible species were identified and this is confirmed by differences in venation and colouration.

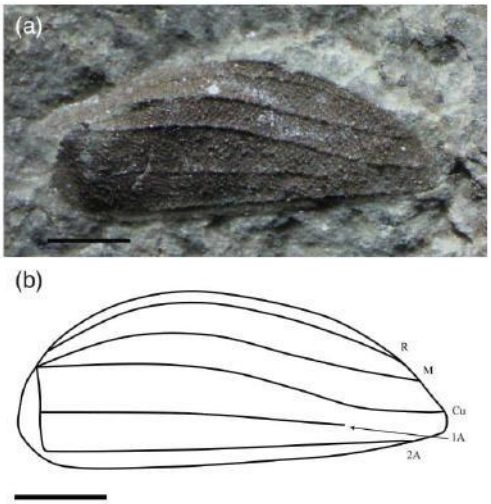

Figure 5 *Phanerogramma heeri* (Giebel, 1856), neotype NHMUK I.10961, Lilstock Formation (Rhaetian), Forthampton, Gloucestershire, England: (a) photo; (b) line drawing. Scale bars = 1 mm.

significantly far away from the central group, indicating a significant size difference; they also vary from the central group in their venation, colour pattern, stratigraphic age and, in some cases, palaeogeography, and so can be regarded as separate new species. The smallest one is from Australia and the largest is the paired tegmina figured by Brodie (1845, fig. 15).

Trachopteryx martynovi Carpenter 1976 (Trachopterygidae) from the Early Permian of Kansas, USA, has a very similar tuberculate ornament to *Phanerogramma* and it has been suggested (David Grimaldi pers. comm. 2015) that they could be related. However, in *Trachopteryx*, R1, Rs, MA, MP, CuA and CuP branch pectinately from a common stem, unlike in the Dermaptera specimens, where the veins originate at the base of the wing. In addition, the anterior margin is straight in *T. martynovi*, but curved in *Phanerogramma*, and the posterior margin is curved in *T. martynovi*, but straight in *Phanerogramma*; thus, it is unlikely that they are closely related.

Phanerogramma heeri (Giebel 1856)
(Fig. 5)

Hemelytron of Homoptera or beetle Brodie 1845, p. 128, pl. 8, figs 17, 18.

Akicera heeri Giebel, 1856, p. 310.

Akicera frauenfeldi Giebel, 1856, p. 310.

Akicera heeri Giebel, Goss 1879, p. 146.

Akicera frauenfeldi Giebel, Goss 1879, p. 146.

Akicera frauenfeldi Giebel, Scudder 1891, p. 104 (no. 611).

Akicera heeri Giebel, Scudder 1891, p. 104 (no. 612).

(?Locustidae) *heeri* Giebel, Handlirsch 1906–08, p. 423.

(?Locustidae) *frauenfeldi* Giebel, Handlirsch 1906–08, p. 423.

Phanerogramma heeri (Giebel) Cockerell 1915, p. 479, pl. 60, fig. 10.

Phanerogramma heeri (Giebel) Carpenter 1992, p. 324.

Unnamed dermapteran Jarzembowski 1999, p. 150–01, fig. 12B.

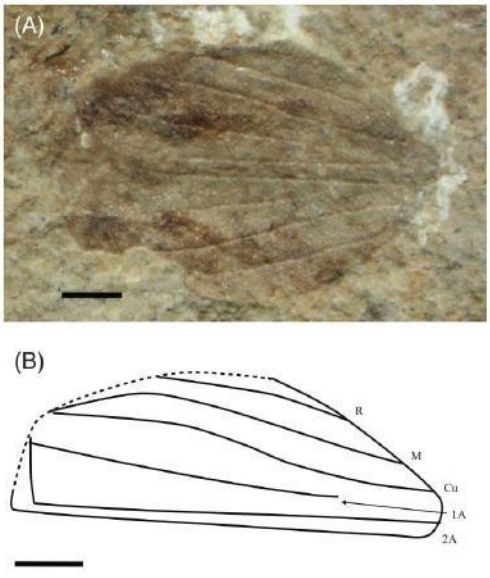

Figure 6 *Phanerogramma gouldsbroughi* sp. nov., holotype, NHMUK I.3578, Rhaetian or Hettangian, from "near Bristol", England: (a) photo; (b) line drawing. Scale bars = 1 mm.

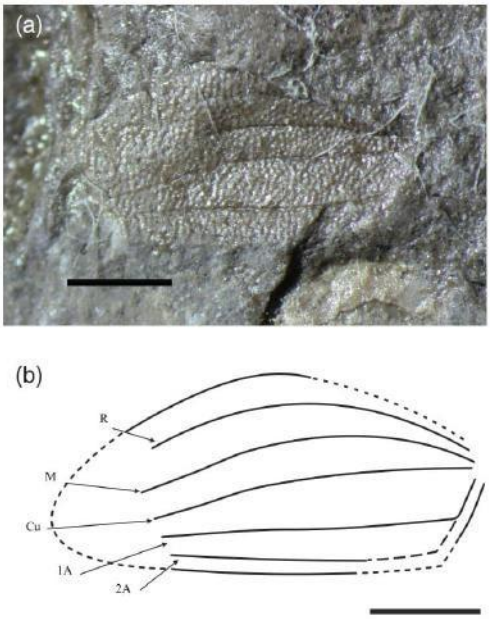

Figure 7 *Phanerogramma australis* sp. nov., holotype, NHMUK In.35044, Blackstone Formation (Carnian), Denmark Hill, Ipswich, Australia: (a) photo; (b) line drawing. Scale bars = 1 mm.

Neotype. NHMUK I.10961, Brodie coll., 'Insect Limestone', Lilstock Formation; Rhaetian; Forthampton, Gloucestershire. Figured by Jarzembowski (1999).

Additional material. NHMUK I.10943, I.11254 Apperley (Rhaetian); USNM 61405 (Lacoe 3452, figured by Cockerell (1915)), NHMUK I.10619, I.10870, Brown's Wood (Rhaetian); NHMUK I.11559 Forthampton (Rhaetian); NHMUK I.11020 Copt Heath (Hettangian); NHMUK I.10985 Morton Bagot (Rhaetian); NHMUK I.11002, I.11004 Norton (Rhaetian); NHMUK I.3569 (Holotype of *P. frauenfeldi*), NHMUK I.10978, I.10981, II.1946 Wainlode (Rhaetian); OUMNH J.55104, MCZ PALE 8667 locality unknown. All Brodie collection, except for: NHMUK II.1946, Jarzembowski coll.; USNM61405, Lacoe coll.; and OUMNH J.55104, Hope coll.

Emended diagnosis. Tegminal length 4.6–6.0 mm, width 1.7–2.3 mm. Evenly pigmented; R running close to C; M and Cu terminate at wing-tip; Cu, 1A and 2A equidistant at base, 2A straight.

Description. Tegmina not truncated, tuberculate, pigmented, with curved anterior margin and straight posterior margin. R faint and simple, runs parallel and close to C, terminating on C just before the tip; M simple, forms a keel at the base, gently curved then straightens out, terminates at tip; Cu simple, originating at same point as M, initially diverges from M then runs parallel to it, converging towards 2A and terminates at tip; A apparently running straight posteriorly with simple 1A branching half-way and fades out, 2A simple, runs parallel to posterior margin and terminates at tip.

Remarks. The figure in Jarzembowski (1999) of the neotype (NHMUK I.10961) is upside down and has been turned the right way up here (anterior margin at top); however, this has resulted in false relief. Cockerell's figure of USNM 61405 appears to show an emarginated tegmen; however, part of the tegmen is missing at that point. The specimens certainly occur in rocks of Rhaetian and Hettangian age and there is nothing to distinguish between them; thus this species crosses the Tr/J boundary.

Phanerogramma gouldsbroughi sp. nov.
(Fig. 6)

Hemelytron of Homoptera or beetle Brodie, 1845, p. 128, pl. 8, fig. 15.

(*Coleopteron*) sp. Handlirsch, 1906–08, p. 457, pl. 41, fig. 75.

Holotype. NHMUK I.3578, Brodie coll., Rhaetian or Hettangian; 'near Bristol' (exact locality and age not known).

Etymology. After S. Gouldsbrough, the lead author's partner.

Diagnosis. Tegminal length 6.8 mm, width 2.8 mm. Differs from *P. heeri* and other species in that it is significantly larger and appears to have a colour pattern. M terminates just before the tip.

Description. Paired tegmina not truncated, tuberculate, pigment pattern, with curved anterior margin and straight posterior margin. R simple, very faint either missing from the left tegmen or mostly obscured on the right; M simple, gently curved then straightens out, terminates just before tip; Cu simple, nearly straight, runs parallel to M, converging towards 2A and terminates at tip; origination of A not visible but assumed to be similar to *A. heeri*; simple 1A merges with 2A on left tegmen, but fades out on right tegmen, thus demonstrating variation; 2A simple, runs parallel to posterior margin and terminates at tip.

Remarks. Cockerell (1915, p. 479) considered this specimen to belong to *P. heeri*; however, the bivariate plot in Figure 4 places this specimen away from the specimens of *P. heeri*. There is a distinct colour pattern present, not seen in any

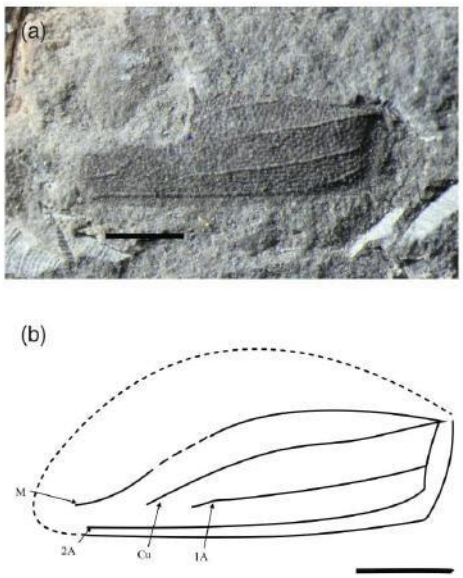

Figure 8 *Phanerogramma dunstani* sp. nov., holotype, NHMUK In.35041, Blackstone Formation (Carnian), Denmark Hill, Ipswich, Australia: (a) photo; (b) line drawing. Scale bars = 1 mm.

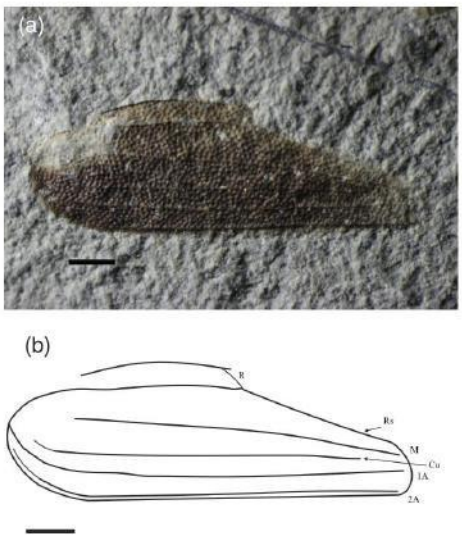

Figure 9 *Dimapteron corami* gen. et sp. nov., holotype, NHMUK I.15008/In.59187 (part and counterpart), Durlston Formation (Berriasian), Durlston Bay, Dorset, England: (a) photo; (b) line drawing. Scale bars = 1 mm.

specimen of *P. heeri*. Thus, based on the currently available evidence, it constitutes a new species.

Phanerogramma australis sp. nov.
(Fig. 7)

Holotype. NHMUK In.35044, Dunstan coll., Denmark Hill Insect Bed, Blackstone Formation; Carnian; Denmark Hill, Ispwich, Queensland, Australia.

Etymology. Latin for southern.

Diagnosis. Estimated tegminal length 4.0 mm, width 1.8 mm. Differs from *P. heeri* and other species in that it is broader, the gap between R and M is wider, and the gap between 1A and 2A is narrower than between Cu and 1A.

Description. Incomplete tegmen missing basal costal margin and tip. Preserved length 3.5 mm, width 1.8 mm. Tuberculate, with curved anterior margin and straight posterior margin. R faint and simple, runs parallel to curved anterior margin and may fade out just before the tip; M simple, gently curved then straightens out, probably terminates at tip; Cu simple, originating at same point as M, initially diverges from M then runs parallel to it, converging towards 2A and probably terminates at tip; A running straight posteriorly with simple 1A branching after half-way and may fade out before tip; 2A simple, runs parallel to posterior margin and probably terminates at tip.

Phanerogramma dunstani sp. nov.
(Fig. 8)

Holotype. NHMUK In.35041, Dunstan coll., Denmark Hill Insect Bed, Blackstone Formation; Carnian; Denmark Hill, Ispwich, Queensland, Australia.

Etymology. After B. Dunstan, as the specimen is from his collection.

Diagnosis. Tegminal length 4.0 mm, estimated width 1.8 mm. Differs from *P. heeri* and other species in that Cu fades out and does not terminate at the wing-tip, and A2 is curved at base.

Description. Incomplete tegmen missing anterior margin. Preserved width 1.5 mm. Tuberculate, with straight posterior margin. R not visible; M simple, curved and converges with 2A, terminates at tip; Cu simple, originating at same point as M, initially diverges from M then runs parallel to it, fading out just after half-way; A apparently running straight posteriorly with simple 1A branching after half-way and fading out; 2A simple, curved at base and runs parallel to posterior margin and terminates at tip.

Dimapteron gen. nov.

Type species. *Dimapteron corami* gen. et sp. nov.

Etymology. After Dr Dima Shcherbakov, who informed AJR that this type of tegmen belongs to Dermaptera.

Diagnosis. Punctate, elongated tegmen with emarginate anterior margin. R merging with C at emargination. Cu simple.

Remarks. This tegmen is generally similar in shape to that of *Sinopalaeodermata neimonggolensis* Zhang, 2002 and *Palaeodermapteron dicranum* Zhao, Shih & Ren, 2011, both within the family Dermapteridae. Zhang (2002) described the ornament of *S. neimonggolensis* as 'puncture'. The tegmen described here differs from these taxa in that C and R merge and Cu is simple. Again, given that the body morphology of *Dimapteron* is not known, it is only tentatively placed in the Dermapteridae.

Dimapteron corami gen. *et* sp. nov.
(Fig. 9)

Dermapteran forewing, Coram *et al.* 1995, p. 150, fig. 15.

Dermapteran (earwig) forewing, Coram & Jepson 2012, p. 29, fig. 26.

Holotype. NHMUK I.15008/In.59187 (part and counterpart), Burnett coll.; Corbula beds, Durlston Formation; Berriasian, Durlston Bay, Dorset.

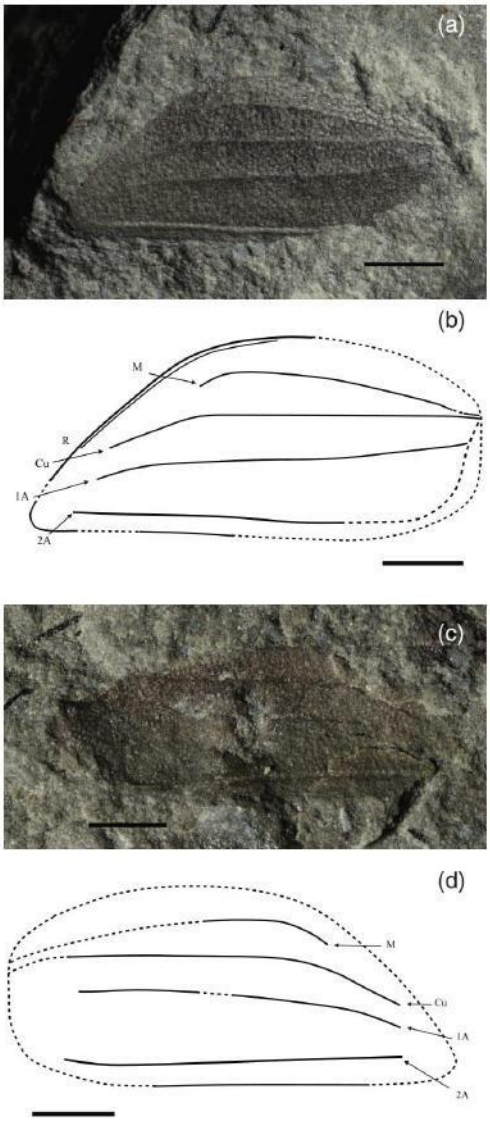

Figure 10 *Valdopteron woodi* gen. et sp. nov., Upper Weald Clay (Barremian), Smokejacks Brickworks, Surrey, England. (a–b) holotype, NHMUK II.3099: (a) photo; (b) line drawing. (c–d) paratype, NHMUK II.3100: (c) photo; (d) line drawing. Scale bars = 1 mm.

Paratype. NHMUK II.3089 Coram coll., Corbula beds, Durlston Formation; Berriasian; Durlston Bay, Dorset.

Etymology. After Rob Coram, who collected the paratype.

Diagnosis. Tegminal length 8.3 mm, tegminal width 4.0 mm. Pigmented with pale spot at anterior base. M, A1 and A2 terminate at tip, Cu fades out just before tip.

Description. Punctate, elongate tegmen, pigmented with pale spot at anterior base, emarginated at two-thirds of length. C curved, merging with R at emargination, then continues straight towards tip; M simple and straight terminating at tip; Cu simple and straight, closer to A1 than M, fades out just before tip; M, Cu and 1A converge towards tip; A1 and A2 simple and straight running parallel to each other and the posterior margin, terminating at tip.

Valdopteron gen. nov.

Type species. *Valdopteron woodi* gen. et sp. nov.

Etymology. Latin for Weald and wing.

Diagnosis. Tegmen punctate, neither truncate nor emarginate, with curved anterior margin straightening towards tip; Rs close to anterior margin; M and Cu almost merge with M running straight towards anterior margin before curving posteriorly; Cu straight basally, gently curved apically; 1A straight along most of its length only slightly curving at the apex; 2A more prominent, straight apically, basal third not known.

Valdopteron woodi gen. *et* sp. nov
(Fig. 10)

Dermaptera Novokshonov *et al.* 2016, p. 47.

Holotype. NHMUK II.3099 [S. 3022a, b] (part and counterpart; Fig. 10 A–C), Jarzembowski coll.; Upper Weald Clay; Barremian; Smokejacks Brickworks, Surrey, England.

Paratype. NHMUK II.3100 [S. 3020a, b] (part and counterpart), Jarzembowski coll.

Additional material. NHMUK II.1856 (1) (part and counterpart), Upper Weald Clay; Barremian; Smokejacks Brickworks, Surrey, England. Coll. 12/06/1996. Incomplete tegmen, tentatively placed in this species.

Etymology. After the late Chris Wood, Cretaceous stratigrapher and journal editor.

Diagnosis. As for genus.

Description. Holotype incomplete, left tegmen with punctate ornament, maximum tegminal length 5.7 mm, tegminal width 2.1 mm (as preserved). Cuticle unpatterned, brown coloured. Anterior margin curved, posterior margin straight. Veins simple except M; Cu and M approaching anteriorly. 2A prominent, slightly flexed anteriorly. 1A less strongly developed, slightly sinuous. Rs submarginal. Veins Rs–1A curved apically at their distal ends.

Family Protodiplatyidae Martynov, 1925

Brevicula Whalley, 1985

Type species. *Brevicula gradus* Whalley, 1985.

Emended diagnosis. Punctate tegmina without venation, reaching third abdominal segment. Posterior margin straight to slightly convex and the anterior margin emarginate. Coxae short, rounded. Ovipositor present in females.

Brevicula gradus Whalley, 1985
(Figs 11, 12)

Brevicula gradus Whalley 1985, pp. 116–17, figs 3–4.

Brevicula gradus Whalley; Ross & Jarzembowski 1993, p. 376.

Brevicula gradus Whalley; Zhang 2002, p. 355.

Brevicula gradus Whalley; Ross 2010, p. 278, pl. 49, fig. 1.

Brevicula gradus Whalley; Jarzembowski & Palmer 2010, p. 174, fig. 4.25.

Brevicula gradus Whalley; Nel *et al.* 2012, p. 191.

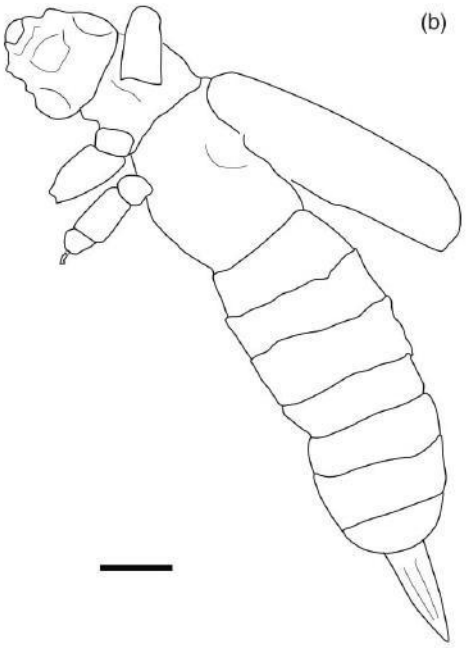

Figure 11 *Brevicula gradus* Whalley, 1985, holotype, NHMUK In.53993, Charmouth Mudstone Formation (Sinemurian), Black Ven, Dorset, England: (a) photo; (b) line drawing. Scale bars = 1 mm.

Holotype. NHMUK In.53993 (part and counterpart), female with ovipositor, Jackson coll., Flatstones, Black Ven Marls; Sinemurian; Black Ven, Dorset.

Paratype. NHMUK In.51036 (part and counterpart), Jackson coll. Female with ovipositor from Woodstones of Black Ven (Sinemurian).

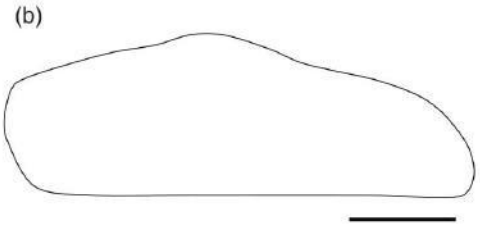

Figure 12 *B. gradus*, isolated tegmen, NHMUK II.3087, Charmouth Mudstone Formation (Sinemurian), Monmouth Beach, Dorset, England: (a) photo; (b) line drawing. Scale bars = 1 mm.

Additional material. NHMUK II.2181, Sole coll. Female with ovipositor from Woodstones of Black Ven (Sinemurian). NHMUK II.3087, II.3088, both Coram coll., Monmouth Beach (Sinemurian).

Emended diagnosis. As for genus, with tegminal posterior margin straight.

Description. (Emended from Whalley 1985). Length (tip of head to tip of ovipositor) 10–12 mm, width of abdomen 2–2.2 mm. Head prognathous; only base of filiform antennae preserved; prothorax rounded; tegmina strongly punctate, elongate; probably reaching third abdominal segment; abdomen parallel sided, with at least six visible segments, terminal segment rounded; legs cursorial, slender, femora slightly thickened, tibia thin, four or five segmented tarsi. Pointed ovipositor in females. Cerci not visible, probably not preserved, which may indicate they were fine and filiform.

Remarks. Whalley (1985) considered this taxon possessed two slender forceps; however, this structure does not appear to be divided and is much more likely to be an ovipositor, as suggested by Nel *et al.* (2012). Although originally described as a dermapteran, Zhang (2002) considered this taxon could "bear more primitive features" than those of other fossil Dermaptera, and considered it could be a staphylinid instead. The presence of the ovipositor of *B. gradus* indicates it is certainly a dermapteran. The presence of older Dermaptera (*Phanerogramma*) indicates that they had certainly appeared by the late Triassic, and more derived forms with no venation could have evolved by the Sinemurian. The presence of an ovipositor and the absence of distinct forceps indicates that this taxon probably only had primitive, simple, filiform cerci (not preserved), typical of the family Protodiplatyidae, such as in *Longicerciata mesozoica* Zhang, 1994 and *Sinoprotodiplatys zhangi* Nel *et al.*, 2012.

Brevicula maculata sp. nov.
(Fig. 13)

Holotype. NHMUK II.3086, Coram coll., *Caenisites turneri* Zone, Sinemurian, Charmouth Mudstone Formation, Monmouth Beach, Dorset.

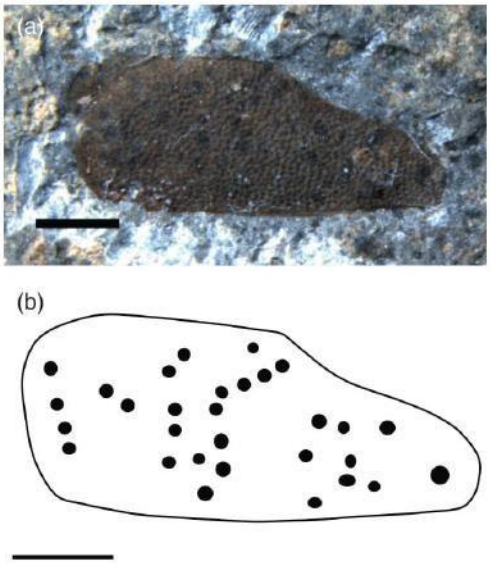

Figure 13 *Brevicula maculata* sp. nov., holotype, NHMUK II.3086, Charmouth Mudstone Formation (Sinemurian), Monmouth Beach, Dorset, England: (a) photo; (b) line drawing. Scale bars = 1 mm.

Etymology. After the presence of spots on the tegmina.

Diagnosis. Tegmina as for genus, with slightly convex posterior margin. Anterior margin straight to just over half of tegminal length then sigmoidally curved to blunt apex. Venation absent; distinct spots present.

Description. Isolated tegmen, length 4.5 mm, width 1.5 mm. Many dark spots visible over tegminal surface.

Remarks. Holotype donated to the NHM by Rob Coram for the purpose of this study. This is the only known fossil earwig specimen with spots.

Dermaptera *incertae sedis*

Remarks. There is one more isolated tegmen known from the Mesozoic of England. It consists of a faint impression, but certainly appears to be different from other fossil taxa; however, in the absence of more characters, it cannot be placed in any family.

Trivenapteron gen. nov.

Type species. *Trivenapteron moorei* gen. et sp. nov.

Diagnosis. Differs from other fossil dermapteran tegmina in that it has three prominent, diverging veins (probably R, M and Cu), plus a simple A vein.

Etymology. Latin for three veins and wing, gender masculine.

Trivenapteron moorei gen. *et* sp. nov.
(Fig. 14)

Earwig tegmen, Williams *et al.* 2015, p. 686.

Holotype. TTNCM 489 Moore coll., Upper Lias; Toarcian; Strawberry Bank, Ilminster, England.

Etymology. After Charles Moore.

Diagnosis. As for genus.

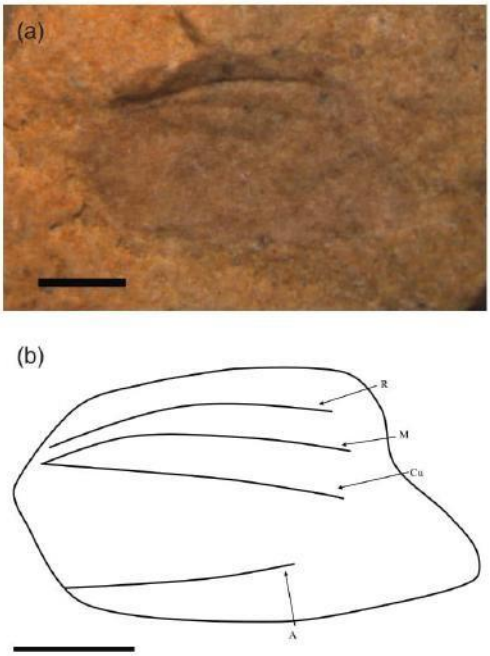

Figure 14 *Trivenapteron moorei* gen. et sp. nov., holotype, TTNCM 489, Upper Lias (Toarcian), Ilminster, Somerset, England: (a) photo; (b) line drawing. Scale bars = 1 mm.

Description. Tegminal length 3.9 mm, tegminal width 2.3 mm. Sub-quadrate, truncate tegmen, pointed apically and without ornament. Three diverging veins, with M and Cu having a common origin, plus a simple A vein running near to the posterior margin.

4. General discussion

This study provides a taxonomy of earwig specimens primarily from UK collections, based on isolated tegmina. *Phanerogramma* is the oldest named dermapteran genus, with *P. australis* and *P. dunstani* the oldest known described species (Carnian).

Previously, the range of the Dermapteridae was within the Jurassic: Callovian to Oxfordian (Nicholson *et al.* 2015); however, if *Phanerogramma, Dimapteron* and *Valdopteron* do belong to this family, then the range is extended from the Triassic: Carnian to Cretaceous: Barremian.

There are vague similarities in the appearance of the tegmina described here and the tegmina of a new proposed order of insects, Alienoptera, described from Cretaceous amber of Myanmar (Bai *et al.* 2016). When attached to a whole specimen, the differences are clear, but there may be some confusion if isolated tegmina are found. There is, as yet, only one specimen of this order known, so current knowledge is limited. There are some key differences that distinguish the orders. Although Bai *et al.* (2016) do not give any specific measurements, the tegmina appear much smaller than those described herein (~2 mm in length). Additionally, these tegmina are more equilaterally sided, appearing more like a triangle, whereas those of earwigs are more elongate. It is not entirely clear in the images provided, but the tegmina do not appear to be

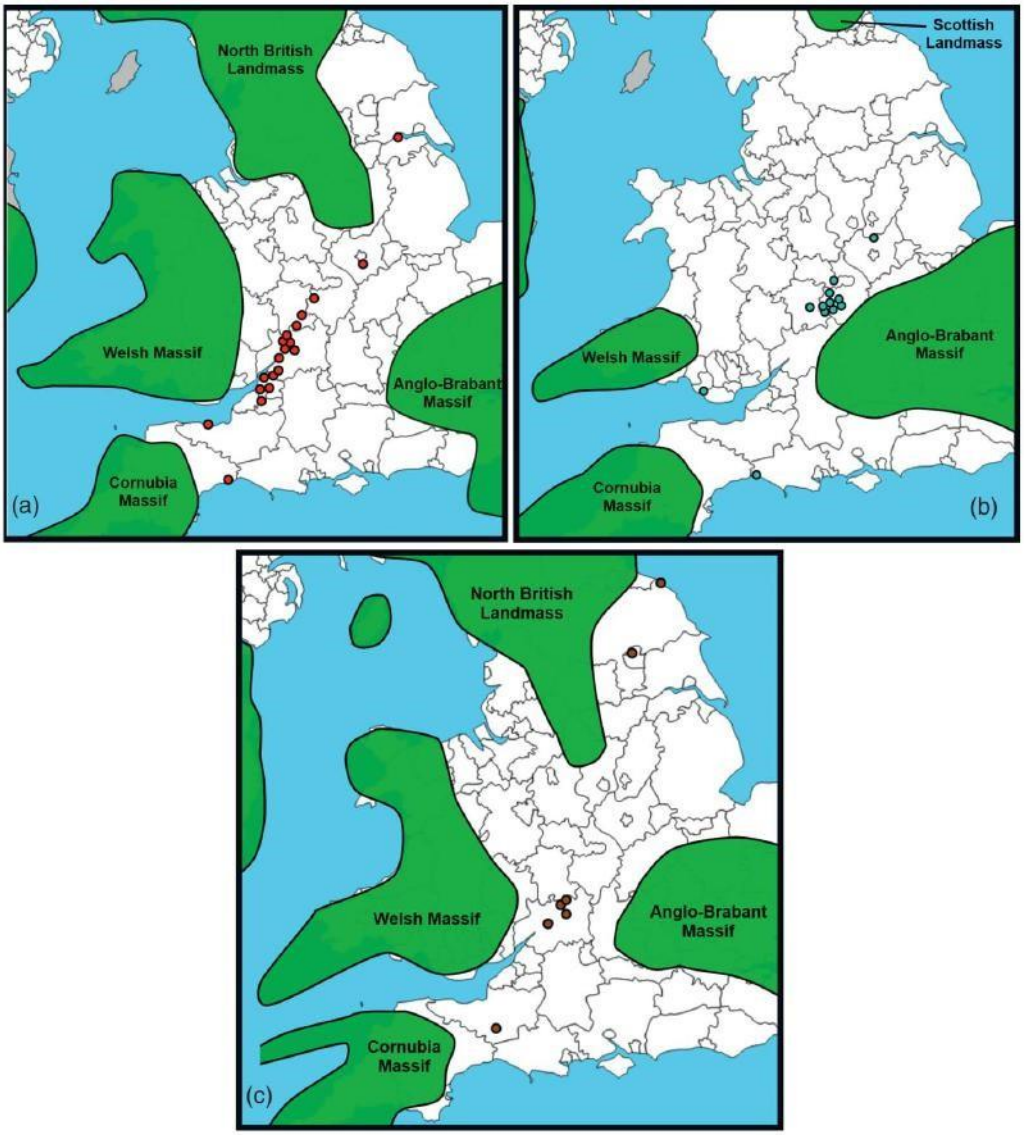

Figure 15 Palaeogeographic maps of the United Kingdom: (a) Rhaetian, modified from Fischer *et al.* (2012) and Benton *et al.* (2002); (b) Hettangian, modified from Simms (2004); (c) Toarcian, modified from Arias (2007) and Stumpf (2016). Coloured dots represent insect-bearing localities for each stage.

ornamented or have venation, and although there are specimens of earwigs without venation, they usually have some form of ornamentation. Therefore, isolated tegmina which are more elongate and which possess ornamentation and/or venation, and especially paired tegmina which evidently come together at the posterior margin, should still be referred to the Dermaptera. Also, the clavus of some heteropterans can look superficially similar to an earwig tegmen when isolated. They are much more elongate than those found on the Alienoptera specimen and more triangular than those found on earwigs.

Today, many earwigs are ground dwelling, living most of their lives in leaf litter, and have low dispersion rates compared with other arthropods (Moerkens *et al.* 2010). It is therefore interesting to find the same genus in both the UK and Australia. Of course, this assumes that the body morphology of the English and Australian species is similar, but this morphology is not known – hopefully, complete specimens will be found one day.

In the late Triassic, the supercontinent of Pangaea started to break up, though at that time Laurasia and Gondwana

were still connected, so *Phanerogramma* could have had a wide distribution. Some modern taxa do have extensive natural ranges, even though they do not distribute readily. For example, *Labidura* is found in Africa, East Asia, East Indies, Australia, South America and southern Europe today (Popham 2000). Even some species have wide distributions, for example, *Forficula auricularia* is found throughout Europe, North Africa and West Asia without human intervention (Crumb *et al.* 1941). Popham (2000) traced the origin of forficuline earwigs to the area which now comprises northeastern South America and northwestern Africa, using current species distribution and continental drift theory, and proposed several distribution routes. In the Late Triassic, South America and Africa lay in between Europe and Australia. Interestingly, Riek (1974) noted the similarity between Late Triassic fossil insect genera of South Africa and Australia, demonstrating that other taxa had wide distributions at that time. It is likely that more Dermaptera tegmina, perhaps related to *Phanerogramma*, are in fossil insect collections elsewhere, but have not been recognised, so they may yet turn up in collections from South America and Africa.

5. Palaeobiogeography of the British earwigs

During the Rhaetian, much of Britain was above sea level, with the North British landmass reaching south to Birmingham, the Welsh massif covering most of Wales, and the Anglo-Brabant massif reaching out towards Swindon in the west and Luton in the north (Poole 1979; Benton *et al.* 2002; Fischer *et al.* 2012), as shown in Figure 15a. Insects were deposited in the Rhaetian sea, under which lay the English Midlands. This sea was often isolated, with marine incursions resulting in fluctuating salinities, and was a generally hostile environment that supported an impoverished fauna (Swift 1995). Insects collected from deposits of this age may have come from any of these landmasses and it is likely that populations were spread across the islands. Some of the insects are complete and probably drowned in the sea, although many specimens are fragmentary and were probably washed into the basin. Insects collected from the marine Hettangian deposits of the Midlands could have come from the Welsh massif, as assumed by Whalley (1985), or more likely from the Anglo–Brabant massif which extended towards the Severn Basin. By this time, the Welsh massif had receded to the west, due to marine transgression, and the North British landmass became a Scottish landmass, reaching just north of Newcastle (Bradshaw *et al.* 1992; Simms 2004), as shown in Figure 15b. Hettangian-age insect deposits are relatively few compared to Rhaetian insect deposits, and are mostly only found in Warwickshire. It is interesting that only this relatively small area has produced insects, especially given the effort put into the collection of fossil insects in this part of the country. Perhaps the water currents of the time concentrated insect debris in the Binton–Grafton–Copt Heath area and deposited them there, or perhaps only in that area were conditions right for the preservation of fossil insects. Insects collected from the Sinemurian deposits of Dorset probably lived on the small Cornubian island which now makes up Devon and Cornwall.

In the Late Triassic, *Phanerogramma* was probably more prevalent on the North British landmass, with smaller populations on the Welsh massif and the Anglo–Brabant massif. During the Hettangian, the receding of the North British landmass to the north, coupled with a dearth of fossil insects collected in the north of England, could explain the apparent decrease in number of *Phanerogramma* specimens from the Hettangian as compared with the Rhaetian.

During the Pliensbachian to Toarcian, it seems that the Welsh massif was larger, extending towards the Midlands, and the Anglo–Brabant massif receded to the east (Arias 2007), as shown in Figure 1c, meaning that insects from this period (including *Trivenapteron moorei* from Ilminster, Somerset) are more likely to have come from the Welsh massif.

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Maps were adapted from d-maps.com:

Figure 1: http://www.d-maps.com/carte.php?num_car=5596&lang=en;

Figure 12: http://www.d-maps.com/carte.php?num_car=2554&lang=en.

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Appendix 4. KELLY, R.S., ROSS, A., and DAVIDSON, P. 2017. *Holcoptera* (Coleoptera) from the Mesozoic of England and the United States. Proceedings of the Geologists' Association, 128:659–674.

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Mesozoic *Holcoptera* (Coleoptera: Coptoclavidae) from England and the United States

Richard S. Kelly[a,b,*], Andrew J. Ross[b,c], Philip Davidson[d]

[a] School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol, BS8 1TQ, UK
[b] Department of Natural Sciences, National Museum of Scotland, Chambers Street, Edinburgh, EH1 1JF, UK
[c] Department of Earth Sciences, Natural History Museum, Cromwell Road, London, SW7 5BD, UK
[d] Charmouth Heritage Coast Centre, Lower Sea Lane, Charmouth, Dorset, DT6 6LL, UK

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ABSTRACT

The impact of mass extinctions on insect evolution is debated, so investigating taxa that span a crisis is important for understanding such large-scale environmental perturbations. The beetle genus *Holcoptera* has been found in deposits from the Late Triassic: Norian to the Early Jurassic: Sinemurian of England and the United States, and possibly Italy. Historical collections of Rev. P.B. Brodie and J.F. Jackson were re-examined and the ages of British localities reviewed, US collections were re-interpreted, and new material from the Dorset Coast was considered. *Holcoptera schlotheimi* and *Holcoptera confluens* are synonymised based on morphological similarities; *Holcoptera giebeli* remains distinct and a new complete specimen confirms the placement of this genus in the family Coptoclavidae. Three new species are described: *Holcoptera pigmentatus* sp. nov. from the Penarth Group of Warwickshire, *Holcoptera alisonae* sp. nov. (based on the rejected neotype of *H. schlotheimi*) from the Lower Lias of Dorset and *Holcoptera solitensis* sp. nov. from the Newark Supergroup of Virginia. *H. schlotheimi* and *H. giebeli* are known from the Late Triassic Penarth Group and Early Jurassic Lias Group and so survived the end-Triassic extinction, whereas *H. alisonae* and *H. pigmentatus* are only known from the Lias Group. *H. solentensis* is the oldest described species in this genus and is not known from any other locality.

1. Introduction

Holcoptera is a charismatic genus of beetles displaying a distinct colour pattern, which is absent from most other fossil beetles. It occurs in the Mesozoic of Laurasia to the west of Tethys (Whalley, 1985, 1986; Huber et al., 2003). Previous authors have had difficulty assigning this genus to a family as only isolated or paired elytra have been previously described. The only known whole specimen was collected recently by PD from the Dorset coast and is herein described, confirming earlier suggestions that *Holcoptera* is a member of the extinct family of aquatic beetles Coptoclavidae. There are three species of *Holcoptera* described in the literature from the Triassic and Jurassic deposits of Europe and North America, namely *Holcoptera giebeli* (Handlirsch, 1907), *Holcoptera schlotheimi* (Giebel, 1856) and *Holcoptera confluens* Cockerell, 1915. Descriptions have often been based on observations of earlier author's figures or on few specimens and therefore previous studies have missed important information. For this study almost all known available specimens of *Holcoptera* were studied first hand by the senior author. Photographs were supplied where specimens could not be visited in person.

Harpalus schlotheimi Giebel, 1856 was described based on two figures in Brodie (1845, pl.6, fig. 28 and pl.10, fig.2) and then was split into two species in different genera: *Holcoptera schlotheimi* and *Holcoëlytrum giebeli* (Handlirsch, 1907 – in 1906-08). These genera were synonymised by Cockerell (1915), priority was given to *Holcoptera*, and several British specimens held in the US were described as a new species *H. confluens*. The synonymisation of these genera was apparently missed by Zeuner (1962) who synonymised the two genera but gave priority to *Holcoëlytrum*. The original synonymisation has priority as discussed by Whalley (1985). Specimens collected from the Portland Formation of Connecticut and the Mount Crosby Formation of Massachusetts were identified by Huber et al. (2003).

Ponomarenko (e.g. Ponomarenko et al., 1999) has previously suggested that these beetles belong to the extinct family of water beetles Coptoclavidae based on isolated elytra. The finding of a

* Corresponding author at: School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Avenue, Bristol, BS8 1TQ, UK.
E-mail address: richard.kelly@bristol.ac.uk (R.S. Kelly).

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whole specimen of *H. giebeli* by PD, which we describe below, has confirmed this placement. The Coptoclavidae are a relatively common component of early Mesozoic assemblages and are known from the Late Triassic: Carnian to the Early Cretaceous: Aptian (Nicholson et al., 2015; supplement). They are known from both larval and adult specimens with the adults having morphological similarities to the extant family of whirligig beetles (Gyrinidae) and it has been postulated that they may be stem-group gyrinids (see Grimaldi and Engel, 2005). A detailed discusson of the history of the family and other known fossils can be found in Ponomarenko et al. (2015).

This paper is the second of a series investigating and revising insect species from around the Triassic-Jurassic boundary (TJB) of the UK. Such detailed revision of species may allow for a more robust analysis of the effects of the end-Triassic extinction event (ETE) on past entomofaunas than previous family-level analyses that found little evidence of an extinction event amongst insects (Nicholson et al., 2015). It is clear from the taxa discussed in this paper that changes in biodiversity across the TJB were complex even in closely related species and not always entirely destructive with several species of *Holcoptera* surviving and the genus increasing in species richness in the period following the ETE. This is similar to the findings of Ponomarenko et al. (2015) who provided evidence of coptoclavid beetles surviving the end-Permian mass extinction.

2. Materials and methods

This study is based on first-hand examination of 128 specimens from British and 134 from North American museums. Of the specimens collected from British deposits, 83 are held at the Natural History Museum, London (NHMUK), 27 at the National Museum Wales, Cardiff (NMW), seven at the Yorkshire Museum, York (YORYM), five at the Warwickshire Museum, Warwick (WARMS), two at the Bristol Museum & Art Gallery (BRSMG), four at the Smithsonian Institution, Washington, DC (USNM), and one at the Harvard Museum of Comparative Zoology, Cambridge, MA (HMCZ). Of the specimens collected from US deposits 67 are held at the Yale Peabody Museum, New Haven, CT (YPM) and two at the Virginia Museum of Natural History, Martinsville (VMNH). One other possible specimen was identified as *H. schlotheimi* from the Norian-Rhaetian of Bergamo, Italy (Whalley, 1986; Bechly, 1997) but it is not clear from the photographs provided by the Museo Civico di Scienze Naturale, Bergamo whether the specimen is conspecific or even congeneric with the material described herein, so it is excluded.

Of the NHMUK Dorset specimens, 51 were collected by James F. Jackson and the other seven by David Sole. Most of the Gloucestershire/Warwickshire/Worcestershire specimens are part of the Brodie collection except for 13 Binton specimens, 12 of which were collected by R.F. Tomes and one by Slatter. The YORYM specimens are also part of the Brodie collection. Most of the NMW specimens were collected during the construction of the Charmouth bypass by a team of volunteers led by Kevin Page including a team from the Booth Museum, except for five which were collected by Jackson. The BRSMG specimens were collected by J.C. Pearce and the WARMS specimens by R.F. Tomes. The HMCZ specimen was collected by Brodie and the USNM specimens are part of the Lacoe collection. The YPM specimens were collected by Phil Huber and the VMNH by their field crew, led by Nick Fraser.

Collections based in the UK were examined between October 2014 and September 2016 and the North American collections were examined in March 2016. During each visit the specimens were studied using the microscope equipment available at each museum and photographs were taken with a stand supporting aNikon D3300 camera with AF-S Micro Nikkor 40 mm macro lens or where available a Leica-type microscope with a digital camera attached. Measurements were taken from photographs using the package ImageJ and the scale of each image calibrated using a standard ruler, each figure contains a 1 mm scale bar. The longest part of the elytra was used for the length measurements and the widest part for the width measurements. Some specimens were too poorly preserved to be accurately measured and so were not analysed.

3. Localities and ages

Holcoptera specimens have been collected from 13 localities in the UK (all in England, Fig. 1) and two in the USA. The two USA localities were discussed by Huber et al. (2003). At the Solite quarry insects were collected from the Cow Branch Formation of the Newark Supergroup, which have been considered Carnian in age but may be early Norian (Muttoni et al., 2004; Furin et al., 2006; Heckert et al., 2012). The North Carolina/Virginia state boundary passes through the quarry and the insects came from the North Carolina part. The lacustrine sequence has been divided into a series of sedimentary cycles (Liutkus-Pierce et al., 2014). Whiteside et al. (2011) estimated an age of ~226 Ma for the Solite quarry based on an assumed early Norian age, according to the updated Triassic timescale of Ogg et al. (2016). Specimens have also been found at the K–F quarry in Connecticut in the Portland Formation and from Horse Race, Massachusetts in the Mount Toby Formation and are thought to be Hettangian–Sinemurian (Huber et al., 2003).

The majority of the English localites are historical and most have not been collected from since the 19th century. Descriptive accounts of specific insect bearing horizons are often vague and only found in historical literature. In this section we present information regarding the specific insect bearing horizons from the historical literature and attempt to update the ages and terminology as accurately as possible to current geological understanding. The Rhaetian localities of Apperley and Forthampton, Gloucestershire, and Brown's Wood, Warwickshire, the Hettangian locality of Binton, Warwickshire, and the Sinemurian locality of Black Ven, Dorset were discussed in Kelly et al. (2017). The other UK localities are described below. The stratigraphy and horizons are outlined in Fig. 2.

3.1. Aust Cliff, South Gloucestershire [ST 565 895-ST 572 901] (Rhaetian)

Aust Cliff has the most productive insect-bearing sediments of Triassic age in Britain (Palmer, 2010) making it an important locality for investigating insects immediately prior to the TJB. The bottom of the cliff exposes the Mercia Mudstone Group (formerly 'Red Marls' or 'Keuper Marls') which has been relatively dated as Norian (Benton et al., 2002). Overlying the Mercia Mudstone Formation is the Blue Anchor Formation (formerly 'Tea Green Marls'). The Blue Anchor Formation begins in the late Norian and ends in the early Rhaetian, succeeded by the Penarth Group (Benton et al., 2002). The lowest rocks in the Penarth Group are the Rhaetic bone bed of the Westbury Formation which is succeeded by layers of mudstone and limestone and the Lower and Upper Pecten beds. Overlying the Westbury Formation is the Cotham Member of the Lilstock Formation which contains the 'insect limestone' in which insects can be found.

3.2. Brockeridge, Gloucestershire [SO 887 385] (Rhaetian)

The insect limestone at this locality has been described as lying approximately '7 feet' (2.1 m) lower than the beds now known to belong to the Planorbis Chronozone and '1 foot' (0.3 m) below the blue limestone 'Ostrea beds' (Brodie, 1845, p.67). The 'Ostrea beds' are also known as the non-ammonite bearing 'pre-planorbis beds'

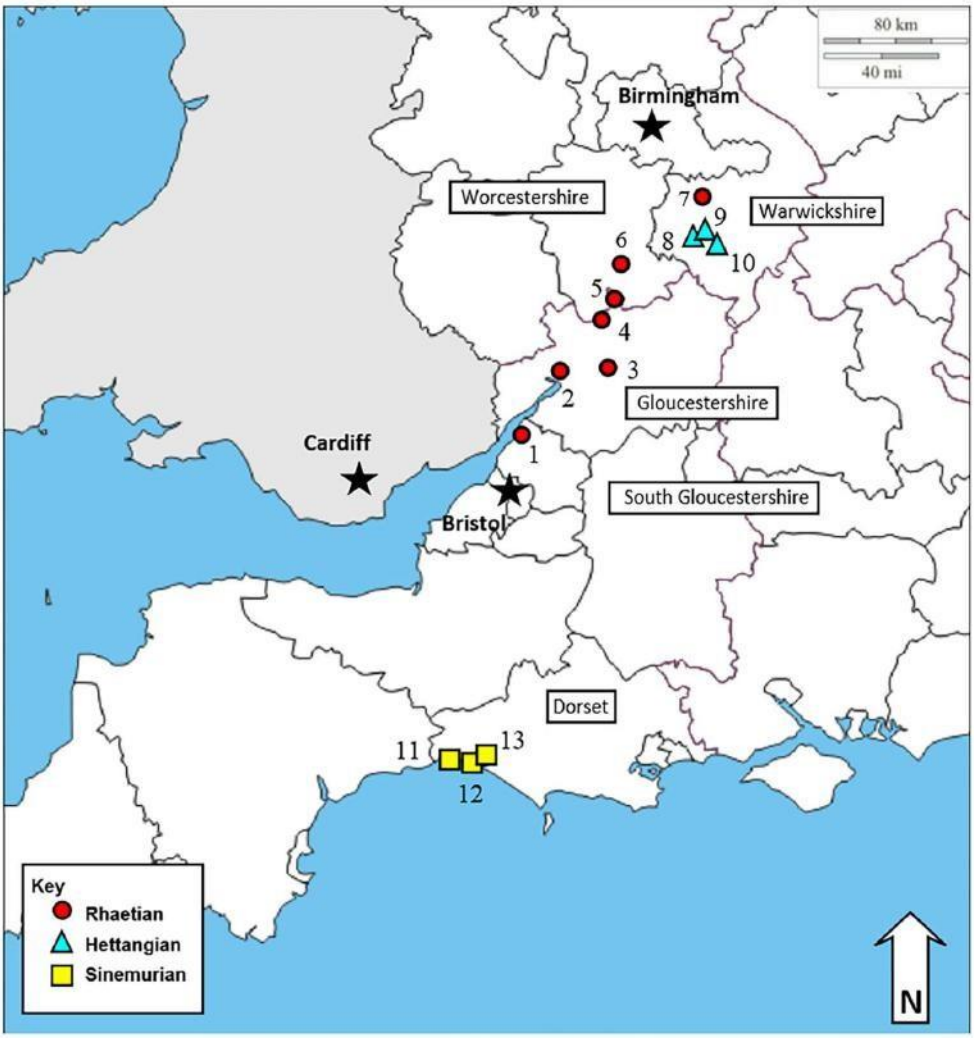

Fig. 1. Localities in England where *Halcoptera* specimens have been collected: (1) Aust, South Gloucestershire; (2) Westbury-on-Severn, Gloucestershire; (3) Apperley, Gloucestershire; (4) Forthampton, Gloucestershire; (5) Brockeridge, Gloucestershire; (6) Strensham, Worcestershire; (7) Brown's Wood, Warwickshire; (8) Binton, Warwickshire; (9) Wilmcote, Warwickshire; (10) Stratford-on-Avon, Warwickshire; (11) Black Ven, Dorset; (12) Stonebarrow, Dorset; (13) Catherston Lane, Charmouth, Dorset.

in the UK (Richardson, 1912) which belong to the Tilmani Chronozone. This zone demarcates the base of the Jurassic system, insects from this locality are found below it and so are Rhaetian in age. Richardson (1903) considered Brodie's 'insect limestone' to be within the Pseudomonotis beds which are thought to be an attenuated form of the Langport Member in Gloucestershire.

3.3. Strensham, Worcestershire [SO 913 406] (Rhaetian)

Insects found at this locality were collected from bed number 18 (Brodie, 1845, p.70). Bed number 4 was within the Planorbis Chronozone and bed number 9 was a 'pre-planorbis' bed now within the Tilmani Chronozone. As the insect limestone (bed 18) is found below these beds then it is of Triassic age. The bottom of the section at Strensham is Rhaetian in age (Ambrose, 2001) and so insects from this locality are also of Rhaetian age.

3.4. Westbury-on-Severn, Gloucestershire [SO 719 129] (Rhaetian)

This locality has also been referred to as 'Garden Cliff' (for example Benton et al., 2002) and is very similar to Aust and Wainlode Cliffs, also in Gloucestershire. The section exposes a transgression from the Norian-aged Keuper Marls through the Rhaetian beds to a very thin layer of 'Lower Lias' at the top of the cliff. Brodie (1845, p.79) placed the insect limestone at bed 2 which is overlain by the 'Ostrea bed' (Tilmani Chronozone). Additionally the insect limestone at this

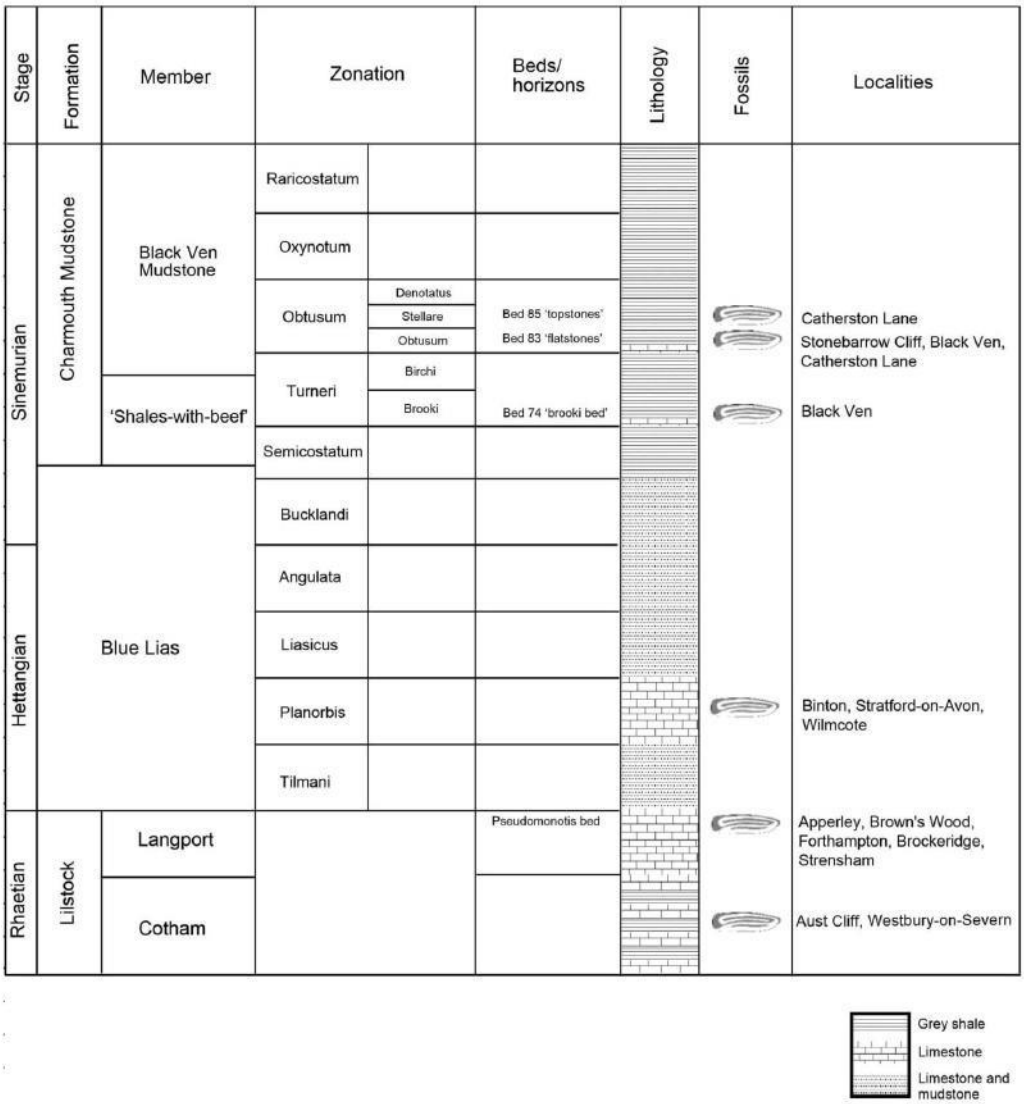

Fig. 2. Stratigraphy of *Holcoptera* bearing localities.
Adapted from Simms et al. 2004 and Page, 2010

locality has been described as lying in the Pseudomonotis bed (Gardiner et al., 1934) which is Rhaetian (Swift, 1995).

3.5. Stratford-on-Avon, Warwickshire [SP 200 550] (Hettangian)

The lowest beds in this area have been described as the 'Ostrea bed' (Tilmani Chronozone), and the lowest limestones as the 'Guinea Bed Limestones' (Ambrose, 2001). The 'Guinea Beds' are now known as the lowest beds of the Wilmcote Limestone Member, which demarcates the lower boundary of the Hettangian. If these are the lowest limestones exposed, then any insects collected from this area are at least Liassic, probably Hettangian as quarries in this area have been described as having what is now known as the Planorbis Chronozone at the top (e.g. Wright, 1860).

3.6. Wilmcote, Warwickshire [SP 161 581] (Hettangian)

The insect limestone is found in similar fashion to that at Binton, Temple Grafton and Bickmarsh (Brodie, 1888, 1897; Richardson, 1906; Kelly et al., 2017), i.e. above the 'Ostrea beds'

(Tilmani Chronozone) and so probably in the Planorbis Chronozone. Wright (1860) described the lowest beds as the 'Guinea Beds' (Wilmcote Limestone Member), and therefore the base of the Hettangian.

3.7. Catherston Lane, Dorset [SY 369 938] (Sinemurian)

This locality was exposed for a short time while the Charmouth bypass was being constructed in 1990 and exposed the Black Ven Mudstone Member of the Charmouth Mudstone Formation (Page, 2008) and so is Sinemuiran in age. Kevin Page was the main scientific lead for the collections and was helped by various volunteers including a group from the Booth Museum headed by Edmund Jarzembowski (Jarzembowski, pers. Comm. April 2017). Insects found at this locality were collected from the Birchi Subchronozone of the Turneri Chronozone (Bed 75) and from the Obtusum Chronozone (Beds 82, 83 h and 85) according to information held at the NMW. *Holcoptera* specimens were collected from indurated tabular limestone lenses in two of these beds, the 'flatstones' in Bed 83 h, at the top of the Obtusum Subchronozone, and the 'topstones' in Bed 85 within the Stellare Subchronozone (Page, 2010).

3.8. Stonebarrow, Dorset [SY 369 929] (Sinemurian)

The stratigraphy of the Dorset coast has been very well documented over the years as it exposes almost the entire Jurassic succession, making it one of the most informative sections found in the UK. East from the Charmouth Heritage Centre is Stonebarrow cliff which exposes the upper part of the Charmouth Mudstone Formation, running from the upper part of the Semicostatum Chronozone of the Sinemurian to the upper boundary of the Davoei Chronozone of the Pliensbachian (Page, 2010; Cope, 2012). The Birchi nodules (Bed 75) are found at the base of the cliff in the Black Ven Mudstone Member (overlain by the Pliensbachian Belemnite Marl Member and the Green Ammonite Member), which have yielded insects but not *Holcoptera* at this locality. *Holcoptera* specimens collected from this locality were found in the 'flatstones' (Bed 83) of the Obtusum Subchronozone (Charmouth Mudstone Formation, Black Ven Mudstone Member, Obtusum Chronozone). The stratigraphy of the Dorset Coast including the history of publication can be found in Page (2010) and a summary of the insects collected from this locality in Ross (2010).

4. Systematic palaeontology

Order Coleoptera Linnaeus, 1758

Family Coptoclavidae Ponomarenko, 1961

Type genus. Coptoclava Ping, 1928

Diagnosis. After Soriano et al. (2007). Divided eyes with a dorsal and ventral part; metepisternum not reaching mesocoxae; metacoxae not broadened anteriorly; transverse metasternal suture absent; meso- and metathoracic legs modified for swimming and tibiae broadened.

Remarks. Fossil beetles are often difficult to accurately place in families, the diversity involved is very high and most are preserved as isolated elytra without the characters essential for familial identification. We assign *Holcoptera* to the aquatic family Coptoclavidae based on whole specimen characters as previously suggested by Prokin et al. (2013) and Ponomarenko in Fedorenko (2014).

A new complete specimen of *H. giebeli* from the Lower Lias of England provides additional morphological characters to enable a fuller description of *Holcoptera*. The ventral aspect of the whole specimen is preserved with two eyes, which suggests another pair was present on the dorsal side. The metepisternum is not entirely clear but the left side does not appear to reach the mesocoxa; right metacoxa not broadened anteriorly; no metasternal transervse suture preserved and at least metatibiae broadened, also possibly mesotibia but this is not entirely preserved. Although there is some broadening of the legs they are not entirely adapted for swimming. Ponomarenko (2003) indicated that early aquatic insects did not have such exaggerated adaptations and mentioned some coptoclavids with two pairs of eyes but no swimming-adapted legs, seemingly similar to *Holcoptera*. On the whole, the characters visible in the new complete specimen are consistent with the diagnosis for the family thus supporting the placement of *Holcoptera* in the Coptoclavidae.

Genus *Holcoptera* Handlirsch, 1907 (in 1906-08)

Type species. Harpalus schlotheimi Giebel, 1856

Emended diagnosis. Elytra entire, covering abdomen, with marked dark and light longitudinal colour bands. One of the bands is consistent in all species, being narrow and running the full length of the elytral suture. Pronotum transverse and narrower than elytra with rounded lateral edges.

4.1. Morphometric analysis

Cockerell (1915) based his assignment of *H. confluens* on a qualitatively perceived size difference and a confluence of dark

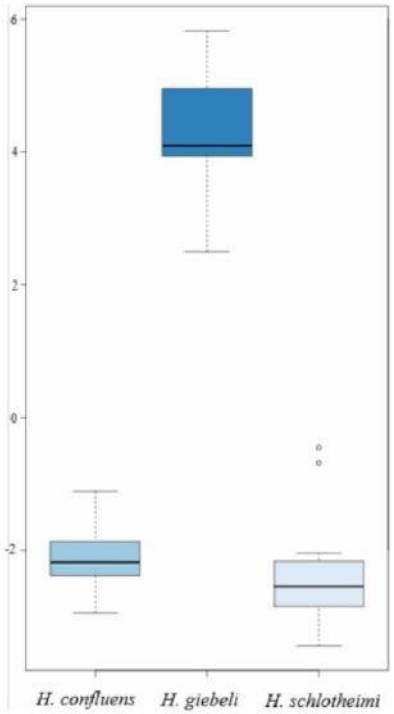

Fig. 3. Results of GLM indicating no significant difference in shape between *H. schlotheimi* and *H. confluens* but a significant difference between both and *H. giebeli*.

bands in the elytral colour patterning compared with *H. schlotheimi*. The differences in colour pattern remains a qualitative problem but the size difference can be assessed quantitatively and although this is not enough evidence in itself for a species assignment or synonymy, it can contribute to evidence for such an action. Therefore, we provide a qualitative description of all specimens as well as a statistical analysis of differences in size between species.

Given the fragmentary nature of the specimens, a full morphometric analysis was not possible, and we present a simpler method using only length and width measurements. The 'prcomp' command was used in the R stats package (R Core Team, 2016) to carry out a principal components analysis (PCA) on the length and width measurements forming a single variable 'shape'. Then the GLM tool was used to apply a general linear model comparing the shapes of the three supposed species.

The GLM indicates a non-significant difference in shape between *H. schlotheimi* and *H. confluens* (GLM, F = 166.89, p = 0.126) and a significant difference in shape between *H. confluens* and *H. giebeli* (GLM, F = 166.89, p = <2e-16) (Fig. 3). These results support a statistically significant difference in shape between *H. schlotheimi/H. confluens* and *H. giebeli*.

Holcoptera schlotheimi (Giebel, 1856)

'Harpalideous Carabidae' Brodie, 1845, pp.101, 124, pl.6, fig.28.

Harpalus Schlotheimi Giebel, 1856, p.63.

Harpalus schlotheimi Giebel, 1856; Scudder, 1891, p.210.

Holcoptera Schlotheimi (Giebel, 1856); Handlirsch, 1907, p.453, pl.41, fig.63.

Holcoptera schlotheimi (Giebel, 1856); Cockerell, 1915, p.480, pl.61, fig.7.

Holcoptera confluens Cockerell, 1915, p.480, pl.61, fig.8. **syn. nov.**

Holcoëlytrum schlotheimi (Giebel, 1856); Zeuner, 1962, p.170, pl.27, fig.5.

Holcoptera schlotheimi (Giebel, 1856); Whalley, 1985, p.173, fig.82.

Holotype. NHMUK I.10783 (Fig. 4), 'Insect limestone' of the Langport Member (Penarth Group: Lilstock Formation); Rhaetian; Apperley, Gloucestershire.

Additional Material.

Rhaetian: NHMUK: I.4000 Apperley; I.10841 Brockeridge; I.11551 Forthampton; I.10975 Strensham. BRSMG: Cd 1387 Westbury-on-Severn; Cd 1348, YORYM: YM1983: 739F, 740F, 741F, 742F, 743F, 744F, 745F Aust Cliff.

Hettangian: NHMUK: I.11007 Stratford-upon-Avon; I.10491 Wilmcote; I.482, I.3365, I.3582, I.6651, I.6653, I.6733,

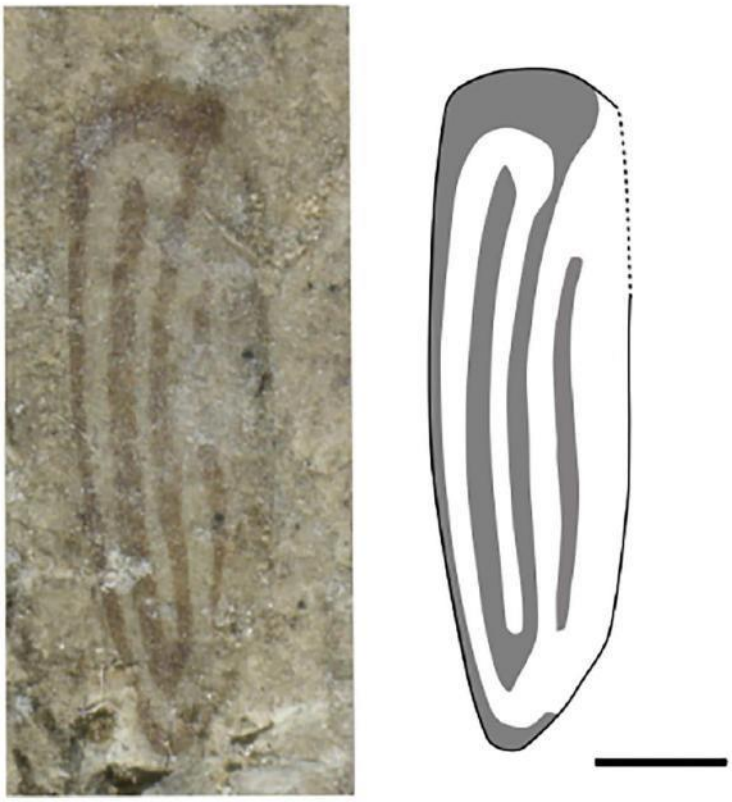

Fig. 4. *Holcoptera schlotheimi* (Giebel, 1856). Holotype NHMUK I.10783. Rhaetian, from Apperley, Gloucestershire.

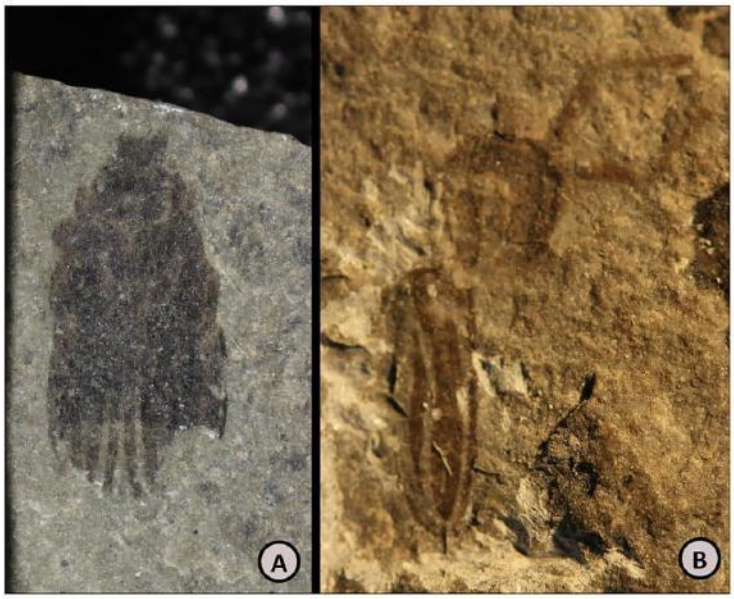

Fig. 5. More complete specimens of *H. schlotheimi*, (A) NHMUK I.11085, (B) NHMUK I.6682. Both Hettangian, from Binton, Warwickshire.

I.6734, I.6735, I.6737, I.6742, I.6743, I.10731, I.6786, I.11085, I.10732, I.10736, I.6682/I.11077 (pt & cpt), WARMS: G 8126: 2, 3, 4, 6, 7 Binton.

Hettangian-Sinemurian: YPM: 202468, 202466, 202467, 202522, 202529, 202541, 202460, 202470, 202469, 202475, 202476, 202482, 202517, 202525, 202542, 202555, 202582, 202459, 202473, 202492, 202516, 202540, 202544, 202458, 202485, 202495, 202507, 202505, 202474, 202462, 202456, 202463, 202536, 202455, 202457, 202477, 202478, 202479, 202484, 202487, 202496, 202497, 202501, 202502, 202503, 202508, 202509, 202523, 202524, 202530, 202548, 202549, 202551, 202552. 202554, 202556, 202557, 202562, 202564, 202577, 202581, 202583, 202584, 202586 2.2 miles SE of Suffield centre, Hartford County, Connecticut, USA (Hettangian-Sinemurian).

Sinemurian: Two additional specimens were collected by James Carroll from Bed 75 of the Turneri Chronozone of Black Ven and are held in his private collection.

Also: HMCZ: PALE 8709; USNM: 61406 (Lacoe 3484) (Cockerell, 1915, fig.7), 61407 (Lacoe: 3482, 3483, 3498) (Cockerell, 1915, fig.8) all from unknown localites in the UK.

Emended diagnosis. Elytra 4.8–7.5 mm long by 1.5–2.7 mm wide with variable but characteristic striped patterning. Four dark bands interspersed with four light bands, though often the darks bands are merged. The 1st (anterior) band is floating, i.e. not connected to other bands or to the base, the 2nd band is connected to a dark patch at the base and the 2nd and 3rd bands are fused distally.

Description of holotype. Single elytron preserved, 5.3 mm in length and 1.6 mm in width. Preservation is faint but characteristic patterning can be seen. There are four dark bands and a dark patch at the base of the elytron, the anterior band is floating, not connected to other bands or the margin, the 2nd band is connected to the dark patch at the base and to the 3rd band at its distal end, the 3rd band has its base floating (not connected), the 4th band is connected to the basal dark patch and runs the full length of the elytron along the posterior margin (elytral suture).

NHMUK I.11085 (Fig. 5a) is a complete beetle with only the legs and antennae missing. Transverse pronotum with slightly curved sides, anterior margin slightly convex. Head prognathous, slightly bigger than pronotum. Two dorsal eyes visible.

NHMUK I.6682/I.11077 (Fig. 5b) consists of an elytron, part of the abdomen and the hind legs. Metafemur and metatibia preserved. Metatibia slightly broadened apically but no evidence of tibial spur. Coxa and tarsi not preserved.

Variation. The colour pattern is highly variable, as demonstrated from a series of specimens from Binton (Fig. 6A–D). The specimens are roughly the same size and given that they are from the same locality (and therefore of the same age) we consider them to be the same species rather than belonging to several species. There are varying degrees of confluence between the dark bands. Some show confluence of bands two and three along some or all of the length, sometimes forming a white hook (Fig. 6B & C). Others are more heavily pigmented with confluence of bands 2–4 (Fig. 6D).

Remarks. The holotype was thought to be lost so a neotype was assigned by Zeuner (1962). However, specimen NHMUK I.10783 has the original figure reference of the holotype (Brodie, 1845, pl.6, fig.28) written on the rock in Brodie's handwriting. The neotype is rejected based on the re-discovery of the holotype, it also does not belong to this species and has been described as a new species herein (see *H. alisonae* sp. nov. Fig. 12).

Holcoptera confluens Cockerell, 1915 was named based on two characteristics, a qualitatively perceived difference in size from *H. schlotheimi*, which has been refuted by the morphometric analysis above, and a confluence of dark bands in the elytral patterning (Cockerell, 1915). The range of specimens from Binton demonstrate that this is a colour variety rather than a separate species. As previously suggested by Zeuner (1962), differences in the relative

Fig. 6. Examples of variation in specimens of *H. schlotheimi*: (A) NHMUK I.10732 (holotype-like); (B) NHMUK I.6737, (C) NHMUK I.6653 (hooked white band); (D) NHMUK I.6786 (heavily pigmented); (E) VMNH 49735; (F) YPM 202459. A–D are Hettangian, from Binton, Warwickshire and E is Hettangian-Sinemurian, from CT, United States.

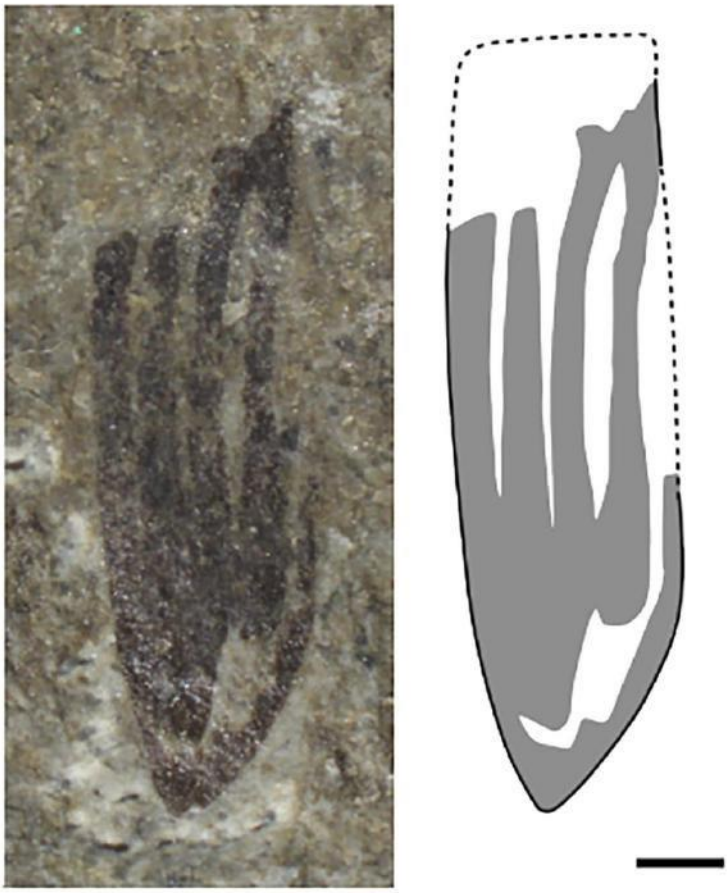

Fig. 7. *Holcoptera giebeli* (Handlirsch, 1907). Holotype NHMUK I.3581. Rhaetian, from Apperley, Gloucestershire.

width of the coloured bands could be caused by variable rock splitting while collecting (sometimes with wider darker bands on the counterpart and narrower on the part) and so is an artefact of the collection process rather than an indication of biological variation. However, this is not apparent in all specimens that have both parts and counterparts, so the colour variation is real.

All of the specimens from the US were identified as *H. giebeli* (Huber et al., 2003). The authors described these specimens as identical to specimens described by Whalley (1985) and Zeuner (1962), only smaller. However, upon examination it is clear, based on the variation discussed herein, that 64 of them belong to *H. schlotheimi* and only three belong to *H. giebeli*. It has also been suggested that the elytral bands are veins (Zeuner, 1962) with Huber et al. (2003) suggesting that in North American specimens veins are preserved black whereas Zeuner (1962) described British specimens as having white veins. There is no structural evidence to indicate that the bands of either colour are veins, neither is there evidence that the bands are caused by variation in elytral thickness and given the variation in *H. schlotheimi* the bands are clearly colouration and not veins.

Holcoptera giebeli (Handlirsch, 1907)

'Harpalideous Carabidae' Brodie, 1845, pp.101, 124, pl.10, fig.2.

Holcoëlytrum giebeli Handlirsch, 1907, p.453, pl.41, fig.64.

Holcoptera giebeli (Handlirsch, 1907); Cockerell, 1915, p.480.

Holcoëlytrum giebeli Handlirsch, 1907; Zeuner, 1962, p.168, pl.27, fig.6-8.

Holcoptera giebeli (Handlirsch, 1907); Whalley, 1985, p. 176, figs 83-87.

Holcoptera giebeli (Handlirsch, 1907); Jarzembowski, 1999, p. 157, fig. 16B.

Holcoptera giebeli (Handlirsch, 1907); Ross, 2010, p. 284, pl. 49, fig. 3.

Holotype. NHMUK I.3581 (Fig. 7), 'Insect limestone' of the Langport Member (Penarth Group: Lilstock Formation); Rhaetian; Apperley, Gloucestershire.

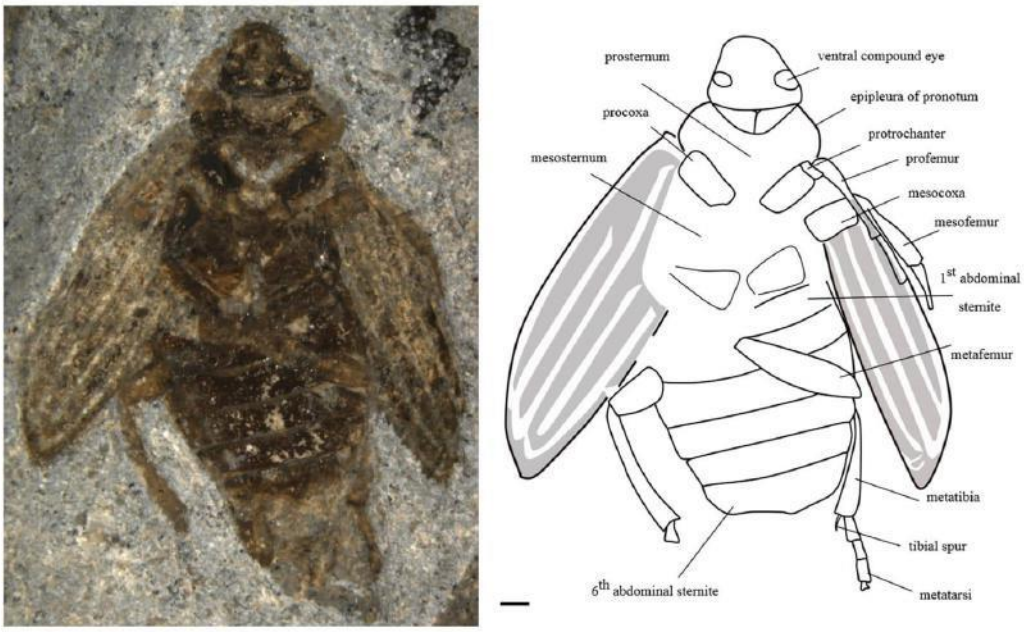

Fig. 8. *Holcoptera giebeli* NHMUK PI II.3101 a, Sinemurian, from Black Ven, Dorset.

Fig. 9. *Holcoptera giebeli* NHMUK PI II.3101 b, Sinemurian, from Black Ven, Dorset.

Additional material.

Rhaetian: NHMUK I.10977 Strensham.

Hettangian: NHMUK I.6771 Binton.

Hettangian-Sinemurian: YPM: 202526, 202506, 202550 Connecticut.

Sinemurian: NHMUK: PI II 2171, PI II 2209 a,b, PI II.3101 (complete specimen), In.49209, In.59100, In.49621, In.49585, In.48163, In.49211, In.49619, In.53943, In.59393, Black Ven; In.49244, In.59117, In.53981 (Whalley, 1985, fig. 86; Ross, 2010, pl. 49, fig. 3), In.53989 (Whalley, 1985, fig. 85; Jarzembowski, 1999, fig. 16B), In.49227, In.64009, In.53985, In.49611, In.64013, In.53937 (Whalley, 1985, figs.83 & 84), In.49229, In.49616 (Zeuner, 1962, pl.27, fig.6), In.51002 (Zeuner, 1962, pl.27, figs.7 & 8), In.49204, In.64012, In.49570, In.59141, In.49563, In.53928 (Whalley, 1985, fig. 87), In.59153, In.49228, In.49239, In.59129, In.59145, In.53962, In.64010, In.53974, In.59148, In.64011, In.49610, In.49219, In.59138, In.59149, In.49618, NMW: 58.552.G1, 65.510.G164, 65.510.G533 a,b, 65.510.G538 a,b Stonebarrow; 65.510.G533 a,b Charmouth; 91.14G.10 a,b, 91.14G.11, 91.14G.12, 91.14G.14 a,b, 91.14G.15 a,b, 91.14G.16, 91.14G.17, 91.14G.18 a,b, 91.14G.19,

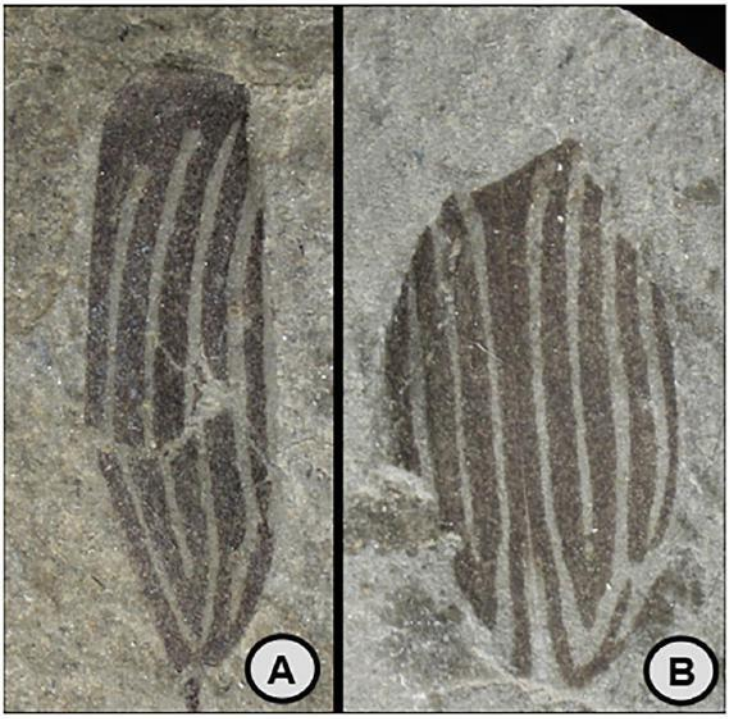

Fig. 10. Additional specimens of *H. giebeli*, (A) NHMUK I.10977. Rhaetian, from Strensham, Worcestershire, (B) NHMUK I.6771. Hettangian, from Binton, Warwickshire.

91.14G.20, 91.14G.21 a,b, 91.14G.22 a,b, 91.14G.24, 91.14G.27, 91.14G.28, 91.14G.32, 91.14G.38 a,b, 91.14G.39 a,b, 91.14G.44, 91.14G.46, 91.14G.47 a,b, 91.14G.9 Catherston Lane. Four specimens from Bed 75 of the Turneri Chronozone of Black Ven and one from the Turneri Chronozone of Monmouth Beach are held in the private collection of James Carroll. Three specimens from the Turneri Chronozone of Monmouth Beach and three specimens from either the Obtusum or Turneri Chronozone of Charmouth are held in the private collection of Rob Coram.

Emended diagnosis. Elytral length 11.6–13.6 mm and width 3.0–4.2 mm; colour pattern is characteristic with five dark bands interspersed with light bands. Dark bands 3 and 4 fuse distally. Pronotum transverse, narrower than elytra with rounded lateral edges. Hind tarsi four segmented, first segment much longer than wide, second segment slightly longer than wide and apical segment wider than long with two hooks. Ventral and dorsal eyes. Tibial spur half the length of first tarsal segment.

Description. Ventral aspect of NHMUK PI II.3101 (Figs. 8 and 9) preserved with elytra distorted so that dorsal elytra are also visible. Specimen is squashed and certain segments have separated causing displacement of body parts and gaps in the overall structure. Total length of 15.5 mm and width of abdomen at widest point 7.5 mm. Elytral length 12 mm, width 4 mm. The elytral pattern is characteristic of *H. giebeli*. No hindwings are preserved. The abdomen has six visible sternites all of which appear to be have been covered completely by the elytra. The epipleura of the pronotum is preserved to each side of the prothorax of which the prosternum is visible. The legs are displaced and are not entirely clear but the pro- and mesocoxae can be seen in part and the metatibia and metacoxa in the counterpart. Also preserved in the part are a trochanter, several femora and tibiae with tibial spur and an almost complete metatarsi. Only one possible metacoxa is preserved in the counterpart but the part does show excavations where the metacoxae would have sat running through the first abdominal sternite laterally towards the elytral epipleura. Metafemur approximately 2 mm, metatibia approximately 2.5 mm expanding towards apex. At least four tarsal segments are present, the first three of almost equal size and the last one much smaller. The head appears prognathous but with no obvious mouthparts preserved, ventral pair of eyes preserved. There is a poorly preserved antenna which seems to show the most apical seven segments with a slight widening to a club in the most apical two segments.

Remarks. Unfortunately the holotype is very incomplete, however the preserved size and colour pattern is consistent with the abundant younger specimens from Dorset (see figs in Zeuner, 1962 and Whalley, 1985). The additional specimen from the Rhaetian is better preserved (Fig. 10a) and is clearly conspecific with specimens from after the TJB (Fig. 10b). The nearly complete specimen was discovered by PD at Black Ven, Charmouth, Dorset, contained within a fragment of an early-diagenetic limestone nodule that had rolled down to the beach. The horizon can be traced with certainty to the Obtusum Subchronozone, Late Sinemurian, as the nodule also contained the diagnostic ammonite *Asteroceras obtusum*. The small section of the nodule containing the specimen was split with geological hammer so the specimen is preserved as part and

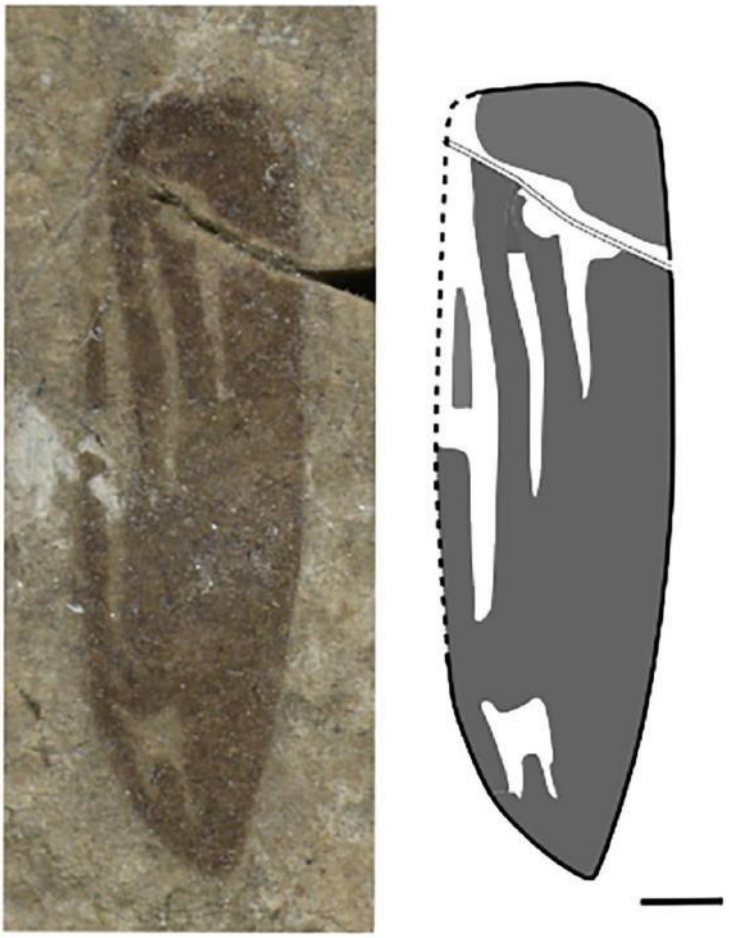

Fig. 11. *Holcoptera pigmentatus* sp. nov. holotype. NHMUK I.10714. Rhaetian, from Brown's Wood, Warwickshire. (A) photo, (B) line drawing.

counterpart. It was then mechanically prepared using an ST air pen by local preparator Chris Moore. The specimen was recorded for the West Dorset Fossil Collecting Code (Ref 324) before being donated for this study.

Holcoptera pigmentatus **sp. nov.**

Holotype. NHMUK I.10714 (Fig. 11). White Lias (Rhaetian); Brown's Wood, Warwickshire; Brodie Coll.

Etymology. After being heavily pigmented.

Diagnosis. Elytral length 9.3 mm, width 2.9 mm. Heavily pigmented, all dark bands fused, with three thin, slightly oblique pale bands getting progressively shorter towards the posterior margin. Pale spot at distal end.

Description. The holotype is an isolated elytron. There is a crack basally and most of the anterior margin is not preserved making it appear as though a fourth white band exists, but this is a preservation artefact rather than a biological characteristic.

Remarks. This specimen is intermediate in size between *H. schlotheimi* and *H. giebeli*. The colour pattern is similar to the heavily pigmented variety of *H. schlotheimi* though it has an extra pale band and pale spot, thus it constitutes a new species. The holotype of *H. giebeli* has broader dark bands than seen in most other specimens, and they slightly fuse though not to the same degree as seen in this specimen. Although there is only one known specimen we consider the unique size and colour pattern as sufficient to warrant the description of a new species.

Holcoptera alisonae **sp. nov.**

'Holcoëlytrum schlotheimi' (Giebel, 1856); Zeuner 1962, p.170, pl.27, fig.5.

'Holcoptera schlotheimi' (Giebel, 1856); Whalley 1985, p.173, fig.82.

'Holcoptera schlotheimi' (Giebel, 1856); Jarzembowski, 1999, p.157, fig. 16A.

'Holcoptera schlotheimi' (Giebel, 1856); Ross, 2010, p.284.

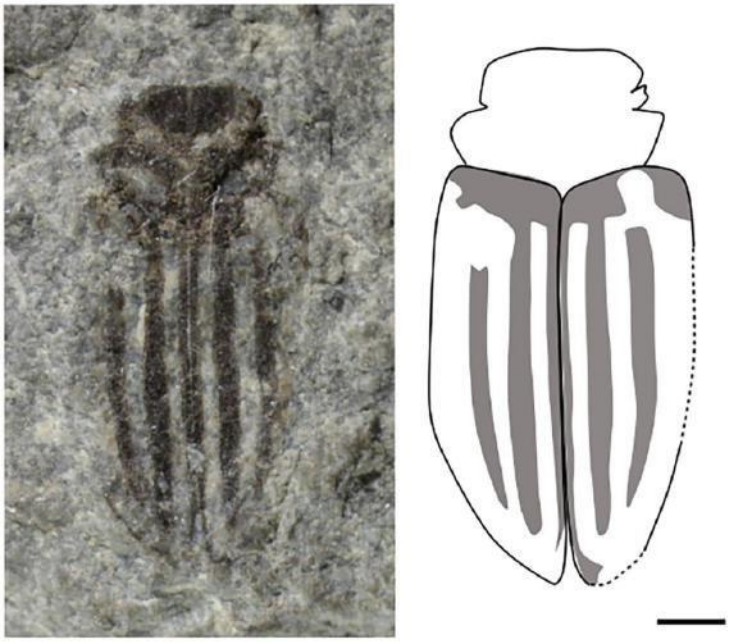

Fig. 12. *Holcoptera alisonae* sp. nov. holotype. NHMUK In.59115. Sinemurian, from Stonebarrow, Dorset.

Holotype. NHMUK In.59115 (Fig. 12). 'Flatstones', Charmouth Mudstone Formation, Lower Lias (Sinemurian), Stonebarrow, Charmouth, Dorset. Jackson Coll. This specimen was the neotype of *Holcoëlytrum schlotheimi* (Giebel, 1856) as assigned by Zeuner (1962), but it is distinct enough from *H. schlotheimi* to warrant description as a new species.

Paratypes. NHMUK In.53958a, b, In.53990a, b (Whalley, 1985, fig.82; Jarzembowski, 1999, fig. 16A) Stonebarrow, (Sinemurian); In.51019a, b from Black Ven, II.2172a, b from the Woodstones of Black Ven, NMW 91.14G.137 from Catherston Road, all Sinemurian.

Additional material. One specimen from Bed 83 of the Obtusum Chronozone of Stonebarrow and one from the Turneri Chronozone of Monmouth Beach are held in the private collection of James Carroll. Six specimens from the Turneri Chronozone of Monmouth Beach are in the private collection of Rob Coram.

Etymology. After Alison Crighton, the senior author's mother.

Diagnosis. Length 5.7–6.6 mm, Width 1.6–1.9 mm. Elytron with three dark longitudinal bands and three white bands. The dark bands do not merge distally; band one is floating; bands two and three connect to a dark patch at the base of the elytron. Band three is narrower and runs next to the elytral suture.

Description. Holotype elytral length 6.5 mm and width 1.6 mm. Indication of pronotum and head are preserved but not well enough to make out any details.

Remarks. This specimen was designated as the neotype of *H. schlotheimi* by Zeuner (1962). Although superficially similar to *H. schlotheimi*, on close examination this species only has three dark bands and they do not merge distally. These specimens are all from the Charmouth Mudstone Formation of Sinemurian age, and so younger than *H. schlotheimi* they also do not demonstrate the same high colour variation.

Holcoptera solitensis **sp. nov.**

Holotype. VMNH 49735/49736 (part & counterpart) (Fig. 13), Cycle 1, Cow Branch Formation, (Early Norian); Solite Quarry, North Carolina, USA.

Paratype. VMNH 51839 (Fig. 14). Cycle 13, Solite Quarry.

Etymology. After the locality of the type material, Solite Quarry.

Diagnosis. Elytra length 5.6–6.5 mm, width 2.2–2.3 mm. Colour pattern with four pigmented bands. Three of the bands are floating, i.e. do not connect with each other. The fourth band runs next to the elytral suture and curves around the basal and distal ends of the elytron.

Remarks. These specimens are the only ones seen where none of the bands connect, either to a colour patch at the base or distally, thus we regard this form as a separate species. This locality demonstrates a peculiar preservation of insects in that body parts, wing veins and colour patterns are preserved as silvery-coloured films. The only other beetle to have been described from this locality so far is the oldest known staphylinid, *Leehermania prorova* Chatzimanolis et al., 2012.

5. Discussion

The genus *Holcoptera* is placed in the Coptoclavidae, an extinct family of water beetles abundant in the Jurassic and Early Cretaceous. A reasonable level of confidence can be placed in this assignment based on a complete specimen from Dorset, England. Previous authors have suggested an association between

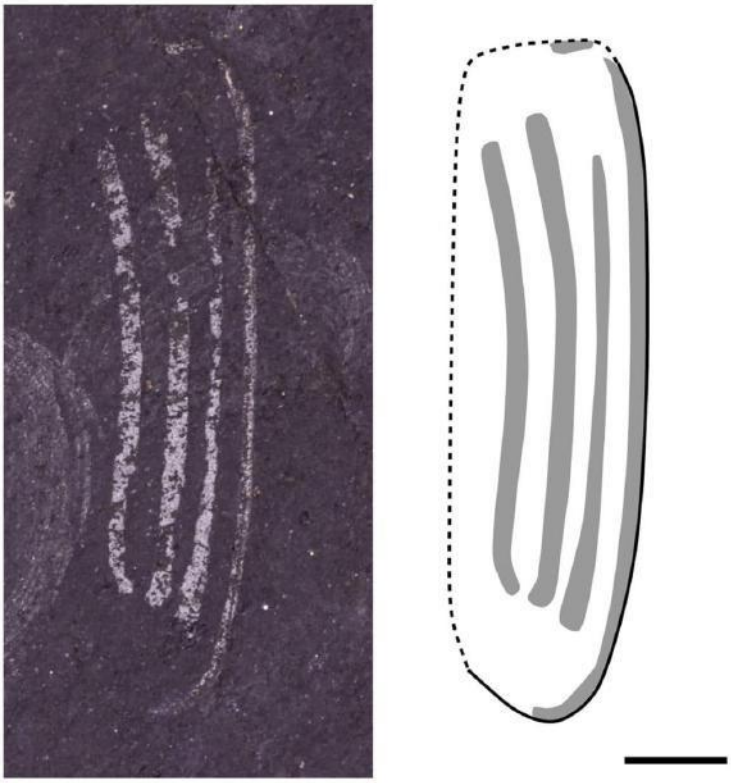

Fig. 13. *Holcoptera solitensis* sp. nov. holotype (part) VMNH 49735. Norian, from the Solite Quarry, North Carolina.

Holcoptera and Coptoclavidae based on isolated elytra. The placement is justified by the presence of divided eyes (assumed by the presence of ventral eyes), metacoxae not broadening anteriorly and at least the metatibia broadened apically, diagnostic features of Coptoclavidae according to Soriano et al. (2007). Also the general similarities in size, shape and elytral ratios as documented by previous authors of coptoclavid species (e.g. Ponomarenko et al., 2005; Ponomarenko et al., 2015).

The genus *Stargelytron* has been described from the Late Triassic of Germany by Ponomarenko et al. (2015) who indicated that the species may belong to *Holcoptera*. Based on the descriptions given, there are some similarities with *Holcoptera* but also differences. The transverse pronotum, size of eyes (*Stargelytron altus*) and overall size are similar but size of the head compared to the pronotum, size of eyes (*Stargelytron larissae*), subtriangular procoxae, short prosternum and ratio of elytral length to width are different. However, several of these differences are also present between the two species of *Stargelytron* and so may be explained by intrageneric variation. Although the new complete specimen is *H. giebeli* rather than the type species, the other species described above are regarded as congeneric due to general similarities in colour pattern and overall elytral shape.

Being found in deposits from the early Norian to the Sinemurian, *Holcoptera* evidently survived the ETE. Specimens were rare in the Late Triassic with only two specimens (both *H. solitensis*) in the Norian (although there may be others, Nick Fraser pers. comm.) and 20 in the Rhaetian, even from deposits that are otherwise productive for insects. Both *H. schlotheimi* and *H. giebeli* crossed the TJB though the majority of Rhaetian-aged specimens are *H. schlotheimi*, with *H. giebeli* not being known in the US before the TJB. It is interesting that both species cross the TJB in England becoming more prevalent in the Early Jurassic, indicating that these beetles may have benefitted from the aftermath of the ETE. The smaller species (*H. schlotheimi*) was much more common immediately after the event in the Hettangian whereas *H. giebeli* was more abundant in the Sinemurian. *H. pigmentatus* is only known from the Rhaetian and *H. alisonae* only known from the Sinemurian. *Holcoptera* have not been found in any of the Toarcian *Lagerstätten* from England or Germany, making it unlikely they were still alive. Whether this was caused by the Early Toarcian mass extinction or if they disappeared earlier is unknown.

Insect bearing Sinemurian deposits are relatively rare and all known occurrences in Europe are from the Jurassic Coast of Dorset. Therefore, most of our knowledge of Sinemurian-aged insects comes from the Jackson and Charmouth Bypass collections held at the NHMUK and NMW, although many additional specimens have been collected more recently by several prolific private collectors such as Rob Coram, David Sole and James Carroll, who provided specimens for this project. Coleoptera are the most common component of the Dorset Sinemurian insect fauna and make up 39% of the Jackson collection (Whalley, 1985). The fragmentary nature of insect fossils means that they are overlooked by many

Fig. 14. *Holcoptera solitensis* sp. nov. paratype VMNH. 51839. Norian, from the Solite Quarry, North Carolina.

collectors looking for larger more attractive fossils, such as ammonites. The profusion of *Holcoptera* compared to other insect genera could reflect their true relative abundance, or it could reflect a preservation bias associated with their hard elytra which are more likely to preserve than more fragile parts of other insects. Additionally, it could be a collection bias because their striped elytra are highly distinctive when compared to other fragmentary insect remains.

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Appendix 5. KELLY, R.S., ROSS, A., and CORAM, R. 2018. Revision of necrotauliids (Trichoptera: Necrotauliidae) from the Triassic/Jurassic of England. Psyche, Article ID 6706120, 12 pages.

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Research Article

A Review of Necrotauliids from the Triassic/Jurassic of England (Trichoptera: Necrotauliidae)

Richard S. Kelly,[1,2] **Andrew J. Ross**,[2,3] **and Robert A. Coram**[1,4]

[1]*School of Earth Sciences, University of Bristol, Life Sciences Building, Tyndall Ave., Bristol BS8 1TQ, UK*
[2]*Department of Natural Sciences, National Museum of Scotland, Chambers St., Edinburgh EH1 1JF, UK*
[3]*Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK*
[4]*British Fossils Unit 2, Bailey Gate Industrial Estate, Sturminster Marshall, Wimborne, Dorset BH21 4DB, UK*

Correspondence should be addressed to Richard S. Kelly; richard.kelly@bristol.ac.uk

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Species previously attributed to Necrotauliidae are revised from the Late Triassic and Early Jurassic of England based on examination of type specimens and non-type material. The necrotauliids have been considered as a basal family of caddisflies (Trichoptera) or as a paraphyletic assemblage of stem-amphiesmenopterans. Herein a new genus, *Austaulius*, is erected which includes all Lilstock Formation\Lower Lias material from England; the previously described species are synonymized with *A. furcatus* and a new species, *A. haustrum*, is described from the Dorset Coast, the holotype of which preserves synapomorphic traits of the Trichoptera not previously described suggesting that the family is trichopteran. The type genus remains *Necrotaulius* and type species *N. parvulus* (Geinitz, 1884) from the type locality of Dobbertin, Germany. One species of *Necrotaulius* is represented in the UK, *N. parvulus*, which is found in the Upper Lias.

1. Introduction

Trichoptera (caddisflies) are a relatively small order of insects with 13,000 living species [1] and 642 fossil species according to Morse [2]. Although more fossil species have been described since, for example, [3], the online Palaeobiology Database (PBDB—http://fossilworks.org) lists 553 valid species. Adults have a similar morphology to moths, highlighting their close relationship with the Lepidoptera. However, whereas Lepidoptera ("scale-winged") have a layer of scales on their wings, Trichoptera ("hairy-winged") usually have a layer of hairs, but there are exceptions and some caddisflies are known to have scales [4]. Most larvae are aquatic although some can be semiaquatic or terrestrial and they are among the few insects to have radiated into the marine realm [5]. Trichopterans from the early Mesozoic are usually preserved as isolated wings and are difficult to distinguish from early Lepidoptera and stem-Amphiesmenoptera.

Trichoptera and Lepidoptera evolved from stem-Amphiesmenoptera early in the Mesozoic [6] with the extinct family Necrotauliidae filling an undefined space within or between the stem-Amphiesmenoptera and the evolving Lepidoptera and Trichoptera. The family Necrotauliidae was erected by Handlirsch [7], who described the genus *Necrotaulius* with seven species, five of which were new, plus two British species named by Giebel [8] that were transferred from the mecopteran (scorpionfly) genus *Orthophlebia*, and the genus *Mesotrichopteridium* with one species, *M. pusillum*. Tillyard [9] made *N. liasinus* (Giebel) a junior synonym of *N. furcatus* (Giebel) and described four new species: *N. westwoodi*, *N. stigmaticus*, *N. apicalis*, and *N. pygmaeus*, from British material. Handlirsch [10] added 10 new species from the Upper Lias (Toarcian) of Germany. He named one species as *N. pygmaeus*, but this was identified as a homonym and renamed *N. ulmeri* [11]. Ansorge [12] transferred *N. parvulus* (Geinitz) from the genus *Orthophlebia* and made *N. pygmaeus* Tillyard, 1933, a junior synonym. Only *Necrotaulius* has been hitherto described from the Triassic/Jurassic of England.

Necrotauliidae has been described as a paraphyletic assemblage of species containing basal Trichoptera, basal Lepidoptera, and advanced stem-Amphiesmenoptera [6, 13].

A revision of the German Upper Lias (Toarcian) material was carried out by Ansorge [12, 14] and several major taxonomic changes were proposed including removing Necrotauliidae from Trichoptera completely. Previously named species within the family from Germany were restricted to *N. parvulus* and *Mesotrichopteridium intermedium* and it was suggested that the latter may not be a necrotauliid [12] but that the Lower Jurassic material from England and Kyrgyzstan needed revising first to properly understand affinities. The genus was likened to *Prorhyacophila* (in Prorhyacophilidae Riek as per [15]) and although the holotype was not examined it was suggested that *Prorhyacophila* was a junior synonym of *Mesotrichopteridium*. The following genera were considered as Lepidoptera by Ansorge [12]: *Archiptilia* Handlirsch; *Epididontus* Handlirsch; *Metarchitaulius* Handlirsch; *Nannotrichopteron* Handlirsch; *Palaeotaulius* Handlirsch; *Pararchitaulius* Handlirsch; *Parataulius* Handlirsch; *Paratrichopteridium* Handlirsch; and *Pseudorthophlebia* Handlirsch. It was reiterated by Ansorge [14] that *Archiptilia*, *Nannotrichopteron*, *Pararchitaulius*, *Parataulius*, and *Pseudorthophlebia* were Lepidoptera because they had scales on the wing surface, and that *Paratrichopteridium* was either a hindwing of *Liadotaulius* or belonged to Lepidoptera. They were all subsequently listed as polyphyletic Necrotauliidae under Lepidoptera [16].

?N. maior, *?Paratrichopteridium areatum*, *Liadotaulius acutipennis*, *P. breve*, and *?P. angustum* were synonymized with *Liadotaulius maior* [12] and it was proposed that this was the oldest known true trichopteran with uncertain familial taxonomy. The genus was provisionally placed in Philopotamidae [17] based on similarities in forewing venation and additional species have been included [18]. A possible philopotamid was described from the Ladinian\Carnian of Madygen, Kyrgyzstan, and prorhyacophilids and necrotauliids have also been described from this locality; thus these are potentially the oldest true Trichoptera (see [19]).

The genus *Acisarcuatus* was described from the Middle Jurassic of China and placed in the Necrotauliidae [20]. The authors were able to include body characteristics which they suggested supported the family's placement in the Trichoptera. The specimen is well preserved, showing genitalia and maxillary palps, and [20] suggested that the presence of harpagones ("claspers") is a synapomorphy of Trichoptera, citing [21, 22]. Both papers do mention the presence of harpagones but neither indicate that this is synapomorphic for the Trichoptera. Even if they meant that the form of the harpagones was synapomorphic (regularly curving towards the middle, narrowing at apex), this would still not be a true synapomorphy as this character is also recorded in other orders such as Diptera [23] and Raphidioptera [24]. Also, multiple variations including 1-segmented and 2-segmented forms and forms which are narrower at the base have been recorded in Trichoptera [22].

The main issue with the higher taxonomy of Trichoptera is that much of the classification is based on larval morphology of extant species. Several characters have been proposed as synapomorphies for Trichoptera and these are listed by Holzenthal et al. [22] as follows: larvae aquatic and apneustic (no open spiracles) so respiration is epidermal, often by filamentous abdominal gills; larval tentorium reduced; larval antennae greatly reduced; larval abdominal segments 1–9 are without ventral prolegs; larval abdominal segment 9 is with dorsal tergite. Only one character was listed as being synapomorphic for adults: the formation of a haustellum, a modified form of mouthparts not seen in any other order. Other authors agree that the haustellum as found in Trichoptera is the only unequivocal autapomorphy of adult Trichoptera [25]. A similar structure is found in in the non-Glossatan Lepidoptera and is assumed to be present in Tarachoptera, but it is small and not visible externally [26]. The haustellum has not previously been reported in any specimen of necrotauliid; coupled with the similarity of wing venation with other basal amphiesmenopterans it has been difficult to say with any degree of certainty whether Necrotauliidae do belong to Trichoptera [18, 20] or are stem-amphiesmenopterans [12, 14].

There is a forewing venation character which has been proposed as diagnostic of the Trichoptera, the CuP tip desclerotised and abruptly bending towards the posterior margin [12]. Kristensen [27] noted the character as potentially important for indicating whether an amphiesmenopteran of uncertain affinity was of the trichopteran lineage or not, but it is not a synapomorphy and is limited in its diagnostic use as it is homoplasious, having evolved separately in different lineages of Trichoptera, some mecopterans (e.g., Bittacidae), and some basal Mecopterida (Microptysmatidae). Not all extant Trichoptera demonstrate this and a curved CuP can also be seen in some species of micro moths (see [28]); thus we do not regard it as a reliable character for separating Trichoptera from Lepidoptera.

Also listed by Liu et al. [20] were *Necropsis* Hong and *Karatauliodes* Sukatsheva; however the former was regarded as belonging to Mecoptera and the latter was designated as a junior synonym of *Necrotaulius* [18]. Zhang et al. [18] also described a new species of *Acisarcuatus* and listed the following additional genera within the Necrotauliidae: *Cretotaulius* Sukatsheva; *Karataulius* Sukatsheva; *Mesotrichopteridium* Handlirsch; *Necrotaulius* Handlirsch; *Pteromixanum* Sukatsheva and Jarzembowski; and *Scyphindusia* Sukatsheva. Of these the latter is based on a larval case so is not useful for a discussion on wings. Carpenter [29] also listed *Liadoptilia* Handlirsch, *Liadotaulius* Handlirsch, and *Phryganeidium* Westwood; however, *Liadoptilia* was regarded as unplaced in Amphiesmenoptera [12] and *Liadotaulius* was tentatively regarded as belonging to the Philopotamidae [18].

Phryganeidium Westwood (erected for *P. pytho* Westwood, 1854 [30] from the Lower Cretaceous of Dorset, UK) has been confused with *Phryganidium* Geinitz (erected for *P. balticum* Geinitz, 1880 [31] from the Lower Jurassic of Germany). It is possible that Geinitz misspelt Westwood's genus, and subsequently *P. pytho* was listed under *Phryganidium* by Scudder (1891, p. 161) [32]. However, Geinitz does not refer to Westwood under the description of *P. balticum*, even though he refers to other trichopteran specimens figured in Brodie, 1845 [33] (*"Orthophlebia" furcata* and *liasina*), and he does refer to Westwood when discussing other new species in the same paper. Geinitz said "Unfortunately, I lack both the necessary literature and a comparative collection of living

insects, and for the time being I have to be modest in using the general family name *Phryganidium* for this genus." This is ambiguous but does not rule out that he was not erecting a new name, and he erects other new generic names in the same paper but does not indicate that they are new. *P. balticum* was moved to the hemipteran genus *Fulgoridium* Handlirsch by Handlirsch (1907, p. 496) [7], where it still resides [34]; and *P. pytho* was placed in the Jurassic trichopteran genus *Mesotrichopteridium* Handlirsch by Handlirsch (1907, p. 616) [7]. *P. pytho* is still a valid species and although Westwood's figures are generally unreliable, his figure of the holotype (pl. 18, Figure 31) clearly shows far fewer branches than *Fulgoridium* and it differs from *Mesotrichopteridium* in having a branched R1. Thus, we regard *Phryganidium* Geinitz (type species *P. balticum*) as a junior synonym of *Fulgoridium* within the order Hemiptera and *Phryganeidium* Westwood (type species *P. pytho*) as a valid genus within the order Trichoptera. *Phryganeidium pytho* has a branched R1 which rejects the species from the Necrotauliidae according to the emended diagnosis provided below. It clearly needs to be redescribed and until that happens we regard it as Trichoptera: family uncertain.

Herein we revise the taxonomy of Late Triassic and Early Jurassic Necrotauliidae from England. Most of these specimens are isolated wings, but several do preserve other body parts including one specimen from the Sinemurian of Dorset in which an external haustellum is preserved suggesting that the Necrotauliidae are trichopterans and not stem-Amphiesmenoptera. A new genus was also found, and although it is imperative to distinguish it from all the other genera listed above, a detailed redescription of these taxa is beyond the scope of this study. A robust definition for the Necrotauliidae based primarily on the type genus *Necrotaulius* is required and we have attempted to supply this based on the examination of some holotypes and non-holotype material and published descriptions. All known species of Necrotauliidae are listed in Table 1 as are the species previously associated with Necrotauliidae but are now excluded.

2. Materials and Methods

There are 57 specimens identified as Necrotauliidae from the Upper Triassic and Lower Jurassic of Britain, all from England. 22 of these are held at the Natural History Museum, London (NHMUK), 15 of which are in the collection of Rev. Peter Bellinger Brodie, two were collected by Edmund Jarzembowski, two by Sydney Buckman, one by David Sole, and two more recently by RAC; 13 are held at the Yorkshire Museum, York (YORYM), all of which are in the Brodie collection; one is held at the Oxford University Museum of Natural History (OUMNH) from the Rev. Hope collection; one is held at the Somerset Heritage Centre for Taunton Museum (TTNCM) from the Charles Moore collection. Additional material was examined from the Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN), the Ernst-Moritz-Arndt Universität, Greifswald (EMAUG), and the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS).

All specimens were examined first-hand by the primary author except where specifically stated. Examinations were carried out using a light microscope (different model at each museum) and photographs were taken with a digital camera attached to a Leica microscope where possible, or with a Nikon D3300 with AF-S Micro Nikkor 40 mm macro lens attached to a stand. Light sources were altered and applied at various angles to capture as much of the preserved venation as possible and where applicable alcohol was used to further highlight venation. Drawings were made from photographs using the Serif DrawPlus X6 graphics package. The locality map (Figure 1) was plotted on the "light grey standard" base map in ArcGIS desktop 10.0; design alterations were made in Serif DrawPlus X6.

2.1. Nomenclatural Acts. The new names contained in this article are available under the International Code of Zoological Nomenclature. This work and the nomenclatural acts it contains have been registered in ZooBank. ZooBank Life Science Identifier (LSID) for this publication is: urn:lsid:zoobank.org:pub: 7528E2B8-E53D-4395-A73F-BAFD3F5A20AF. The LSID registration and any associated information can be viewed in a web browser by adding the LSID to the prefix "http://zoobank.org/."

3. Localities and Ages

Necrotauliids have been collected from 12 localities in the UK all of which are found in England (Figure 1). Most of these localities (those that are inland) are historical and have not been collected from for over 100 years. The literature for the stratigraphy of the insect bearing horizons is equally outdated and so we aim to update the ages of these historical localities to current geological nomenclature. The Rhaetian localities of Brown's Wood, Warwickshire and Apperley, Forthampton, and Wainlode Cliff (Gloucestershire) along with the Hettangian localities of Binton (Warwickshire) and Copt Heath (Birmingham) and the Toarcian locality of Strawberry Bank, Ilminster (Somerset), were previously discussed [35]. The Rhaetian localities of Aust Cliff and Brockeridge (Gloucestershire) and the Sinemurian locality of Monmouth Beach, Lyme Regis (Dorset) were also previously discussed [36]. The localities not previously discussed are described below.

3.1. Blue Anchor, Somerset [National Grid Reference ST 033 435] (Rhaetian). A section at this coastal locality was described and figured by Hauser and Martill [37] showing the succession from the Norian Mercia Mudstone Formation through the entire Rhaetian and into the Lower Lias Blue Lias Formation at the top of the cliff. This is the type locality for the lower Rhaetian Blue Anchor Formation [38]. Several insects have been collected from this site by RAC from loose rocks on the foreshore which are consistent with the limestones of the Cotham Member of the Lilstock Formation.

3.2. Dumbleton/Alderton, Gloucestershire [SP 006 345] (Toarcian). There are several hills in Gloucestershire from which Toarcian aged insects have been collected and the most

Table 1: Known species of Necrotauliidae and previous species now associated with the lepidopteran lineage. T_3: Late Triassic; J_1: Early Jurassic; J_2: Middle Jurassic; J_3: Late Jurassic; K_1: Early Cretaceous.

Genus	Species	Author	Age	Locality
Trichoptera: Necrotauliidae				
Acisarcuatus	*locellatus*	Zhang et al., 2016	J_2	Daohugou, China
Acisarcuatus	*variradius*	Liu et al., 2014	J_2	Daohugou, China
Austaulius	*furcatus*	(Giebel, 1856)	T_3	Aust Cliff, UK
Austaulius	*haustrum*	sp. nov.	J_1	Monmouth Beach, UK
Cretotaulius	*ultimus*	Sukatsheva, 1982	J_3	Unda, Russia
Karataulius	*aeternus*	Sukatsheva, 1968	J_2/J_3	Karatau, Kazakhstan
Mesotrichopteridium	*intermedium*	(Handlirsch, 1907)	J_1	Dobbertin, Germany
Necrotaulius	*fascialatus*	Hong, 1983	J_2	Xiaofanzhangzi, China
Necrotaulius	*kritus*	Lin, 1986	J_3	Zhongshan, China
Necrotaulius	*kubekovi*	Sukatsheva, 1985	J_2	Kubekovo, Russia
Necrotaulius	*mantellorum*	Jarzembowski, 1991	K_1	Capel, UK
Necrotaulius	*minutissimus*	Sukatsheva, 1990	J_3	Daya, Russia
Necrotaulius	*minutus*	(Sukatsheva, 1968)	J_2/J_3	Karatau, Kazakhstan
Necrotaulius	*parvulus*	(Geinitz, 1884)	J_1	Dobbertin, Germany
Necrotaulius	*proximus*	Sukatsheva, 1973	T_2/T_3	Madygen, Kyrgyzstan
Necrotaulius	*qingshilaense*	Hong, 1984	K_1	Shidongzi, China
Necrotaulius	*tener*	Sukatsheva, 1990	J_3	Unda, Russia
Prorhyacophila	*colliveri*	Riek, 1955	T_3	Mt. Crosby, Australia
Prorhyacophila	*furcata*	Sukatsheva, 1973	T_2/T_3	Madygen, Kyrgyzstan
Pteromixanum	*inviolatum*	Sukatsheva & Jarzembowski, 2001	K_1	Durlston Bay, UK
Pteromixanum	*poxwellense*	Sukatsheva & Jarzembowski, 2001	K_1	Poxwell, UK
Pteromixanum	*purbeckianum*	Sukatsheva & Jarzembowski, 2001	K_1	Durlston Bay, UK
Pteromixanum	*ruderatum*	Sukatsheva & Jarzembowski, 2001	K_1	Durlston Bay, UK
Scyphindusia	*hydroptiliformis*	Sukatsheva, 1985	J_2/J_3	Bolshoy, Russia
Trichoptera: family uncertain				
Phryganeidium	*pytho*	Westwood, 1854	K_1	Durlston Bay, UK
Lepidoptera: family uncertain				
Architipula	*ovata*	Handlirsch, 1939	J_1	Dobbertin, Germany
Epididontus	*geinitzianus*	Handlirsch, 1939	J_1	Dobbertin, Germany
Metarchitaulius	*longus*	Handlirsch, 1939	J_1	Dobbertin, Germany
Nannotrichopteron	*gracile*	Handlirsch, 1907	J_1	Dobbertin, Germany
Palaeotaulius	*vicinus*	Handlirsch, 1939	J_1	Dobbertin, Germany
Pararchitaulius	*ovalis*	Handlirsch, 1939	J_1	Dobbertin, Germany
Parataulius	*jurassicus*	Handlirsch, 1939	J_1	Dobbertin, Germany
Pseudorthophlebia	*platyptera*	Handlirsch, 1907	J_1	Dobbertin, Germany
Amphiesmenoptera				
Paratrichopteridium	*efossum*	Handlirsch, 1939	J_1	Dobbertin, Germany
Paratrichopteridium	*costale*	Handlirsch, 1939	J_1	Dobbertin, Germany

productive are in the Dumbleton-Alderton area, although there has been some confusion over the names of the locality/ies. "Dumbleton" and "Alderton" have been described as separate localities [33] but this is not the case even though there are two hills in the area, "Alderton Hill" and "Dumbleton Hill." After seeking consultation from Michael Simms, a geologist local to the area, Palmer [39] treated them as the same locality, indicating that "Dumbleton pit" was not actually on Dumbleton Hill and was only 100 m away from "Alderton Hill quarry." Either way the insect horizon in both the pit and the quarry occupy the same stratigraphic position. Alderton/Dumbleton is a well-known locality for insects from the lower Toarcian fish beds ("Fish and insect beds", "Saurian and fish beds") which are found in the Whitby Mudstone Formation [40]. The fish beds are described as laminated limestone nodules overlaying paper shales [41] and are

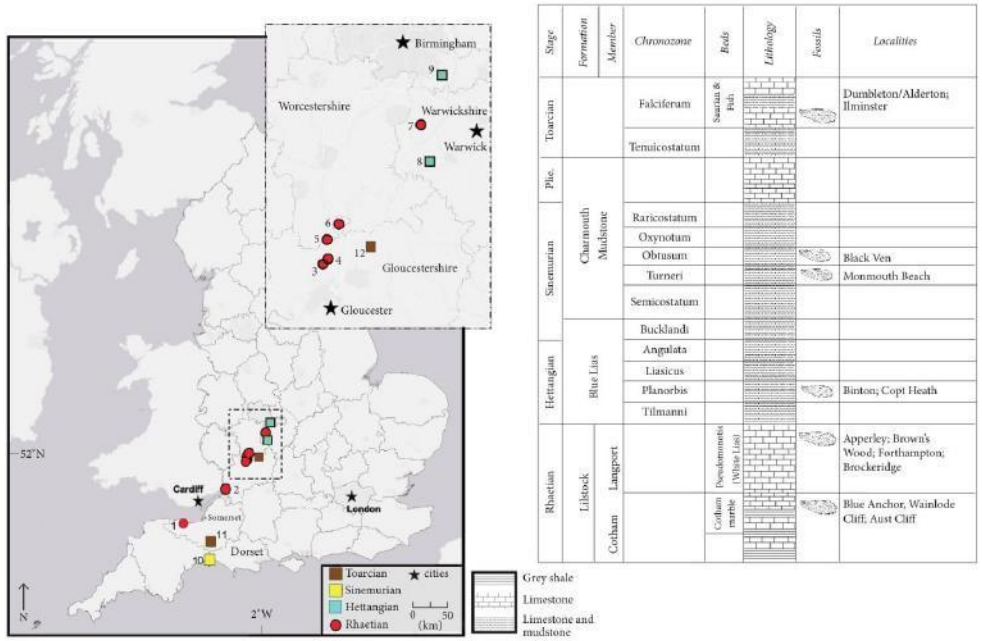

FIGURE 1: Locality map. (1) Blue Anchor, (2) Aust Cliff, (3) Wainlode Cliff, (4) Apperley, (5) Forthampton, (6) Brockeridge, (7) Brown's Wood, (8) Binton, (9) Copt Heath, (10) Monmouth Beach, (11) Ilminster, and (12) Alderton Hill/Dumbleton Pit.

contiguous with the fish beds found at Ilminster [42] being found in the *falciferum* Ammonite Zone.

4. Systematic Palaeontology

Superorder Amphiesmenoptera Kiriakoff, 1948 [43]

Order Trichoptera Kirby, 1813 [44]

Family Necrotauliidae Handlirsch, 1907 [7]

=Prorhyacophilidae Riek, 1955 [45]

Emended Diagnosis. Forewings with the following combination of characters: R1 simple; Rs with two forks (each with two branches); M with two forks (each with two branches); CuA forked; m-cu cross-vein (or base of CuA) present; anal veins 2 and 3 merge, then merge with A1 which terminates on the posterior margin. In hindwing, MP simple and anal veins are simple, terminating on the posterior margin. Hairs present on forewing and around wing-margins of both fore- and hindwings (if preserved).

Discussion. Ansorge [12] considered *Prorhyacophila* a junior synonym of *Mesotrichopteridium*; however this has not been followed by others. Certainly, from the diagnosis provided above it is not possible to exclude the type species *Prorhyacophila colliveri* Riek, 1955 from the Necrotauliidae; thus the family Prorhyacophilidae needs to be regarded as a junior synonym. *Prorhyacophila* and *Mesotrichopteridium* differ in the positions of cross-veins so are kept separate here. The Permian species *Prorhyacophila rasnitsyni* Sukatsheva & Aristov, 2013 in [15, Figure 68(e)] has a branched R1 thus it is rejected from the Necrotauliidae and *Prorhyacophila*.

Description. In addition to the diagnosis of the forewing Sc is either simple or with one or two anterior oblique branches; Sc-r, r-m, m-cua, cua-cup, and al-a2 cross-veins may be present, though may not be visible on poorly preserved specimens.

Remarks. Hairs are not always preserved as most specimens are not well preserved but there are examples of both *Necrotaulius* and *Austaulius* with hairs (Figures 2(b)–2(d)). The family is extinct and only known from the Triassic to Cretaceous but as only preserved characters can be included in the diagnosis there may be superficial similarity with some extant taxa.

Genus *Necrotaulius* Handlirsch [7]

Type Species. Necrotaulius parvulus (Geinitz, 1884) [46]

Emended Diagnosis. Sc simple, r-m cross-vein absent, CuA connected by "Y-shape" to M and CuP; labial palps longer,

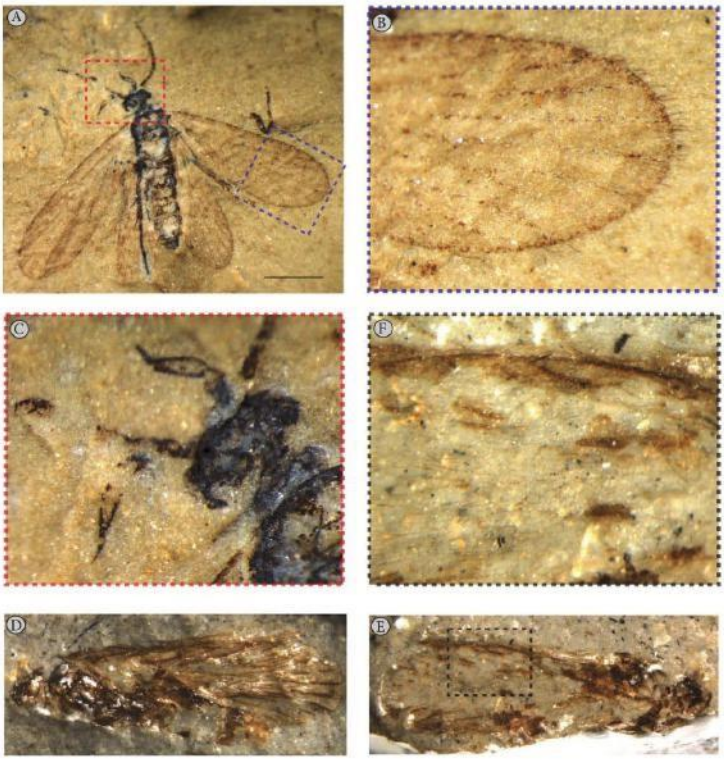

FIGURE 2: Two examples of necrotauliid wings with hairs and labial palps: (a) *Necrotaulius tener* Sukatsheva, 1990 from Daya, Russia (PIN 3015/819); (b) hairs; (c) labial palps; (d) *Austaulius furcatus* (NHMUK II 3104 a); (e) counterpart NHMUK II 3104 b; (f) hairs on NHMUK II 3104 b magnified.

second segment more elongate than first or third (Figure 2(c)).

Remarks. The apex of CuP does not seem to be desclerotised in the British specimens of this genus and more gently curves towards the posterior margin

Necrotaulius parvulus (Geinitz, 1884) [46]

Holotype. EMAUG 119/7 (see [12]) from the Falciferum Chronozone of the Posidonia Shale Formation (lower Toarcian), Schwinz near Dobbertin, Germany.

Additional Material. See [12] for list of lower Toarcian German specimens. British Toarcian: NHMUK I.15014 (holotype of *Necrotaulius pygmaeus* Tillyard, Figure 3) and I.11425, both Dumbleton and TTNCM 39/2011/0733, Ilminster, Somerset.

Remarks. The three British specimens match the diagnosis and description of this species as provided by Ansorge [12]. Sohn et al. [16] indicated that Ansorge [12] redefined *Necrotaulius* to only include the type species *N. dobbertinensis* but this is incorrect. Ansorge designated *N. dobbertinensis* a junior synonym of *N. parvulus* based on the latter's date priority.

Genus *Austaulius* gen. nov.

urn:lsid:zoobank.org:act:D1FBC755-D8BD-45DA-9934-9C78F029DF8E

Type Species. Austaulius furcatus (Giebel, 1856) [8]

Etymology. Aust- after the holotype locality for the type species, and *-taulius* after the suffix for *Necrotaulius*.

Diagnosis. Sc with 1 anterior branch, r-m cross-vein absent, CuA fuses with M for a short distance near the base then with an oblique cross-vein connecting MP + CuA to CuP; labial palps shorter; second segment about same length as first segment (Figure 4).

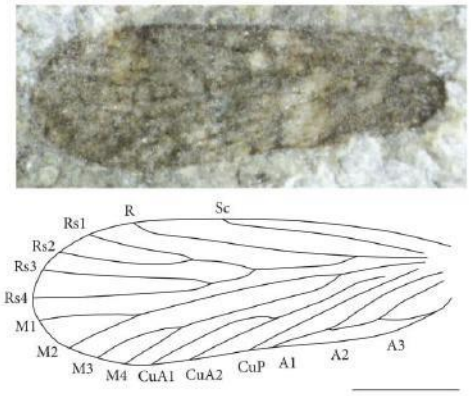

FIGURE 3: Example of English *Necrotaulius parvulus* (Geinitz, 1884), NHMUK I.15014 from Dumbleton pit, Gloucestershire (previous holotype of *Necrotaulius pygmaeus* Tillyard, 1933). Scale bar = 1 mm.

Remarks. Clearly the form of CuA was misinterpreted by Tillyard [9] and begs the question as to whether any other *Necrotaulius* species have been misinterpreted. Other *Necrotaulius* holotypes were checked in person by the senior author. The following do not possess the diagnostic form of CuA as seen in *Austaulius*: *N. parvulus* (Geinitz) (EMAUG 119/7) from the Upper Lias of Germany; *N. kubekovi* Sukatsheva (PIN 1255/193) from the Middle Jurassic of Russia; *N. minutissimus* Sukatsheva (PIN 3063/742), *N. minutus* (Sukatsheva) (PIN 2066/1303), and *N. tener* Sukatsheva (PIN 3015/819) (Figures 2(a)–2(c); also figured in [6], Figure 13.1 and [13], Figure 283) from the Late Jurassic of Russia and Kazakhstan and *N. kritus* Lin (NIGPAS 70078) from the Middle Jurassic of China. *N. fascialatus* Hong and *N. qingshilaense* Hong were described from the Late Jurassic and Early Cretaceous of China, respectively. Unfortunately, it is not known where Hong's holotypes are although researchers at NIGPAS have been searching for them (Wang Bo, pers. comm., 2016). Based on Hong's figures it appears that the basal area of the wing is not preserved in *N. fascialatus* ([47], Figure 46); the character may be present in *N. qingshilaense* ([47], Figure 47) but it is not at all clear; the holotype would need to be examined. *N. mantellorum* Jarzembowski (Booth Museum, Brighton 014897/8) was described from the Early Cretaceous of England [48]. It requires reexamination to confirm whether it belongs to *Necrotaulius* or not. One specimen (NHMUK II 3104 a and b) was identified as *Austaulius* sp. indet. and is included because it preserves hair on the wings (Figures 2(d)–2(f)).

Austaulius furcatus (Giebel, 1856) [8] *comb. nov.*

"Neuropterous insects" Westwood in Brodie (1845) [33], p. 127, pl. 9, Figures 16 and 17.

Orthophlebia furcata Giebel, 1856 [8] p. 261.

Orthophlebia liasina Giebel, 1856 [8] p. 261.

Orthophlebia furcata Giebel; Goss (1879) [49], p. 145.

Orthophlebia liasina Giebel; Goss (1879) [49], p. 145.

Orthophlebia furcata Giebel; Scudder (1891) [32], p. 156 (nos. 1024, 1025).

Orthophlebia liasina Giebel; Scudder (1891) [32], p. 157 (no. 1029).

Orthophlebia furcata Giebel; Woodward (1893) [50], p. 367.

Orthophlebia liasina Giebel; Woodward (1893) [50], p. 367.

Necrotaulius furcatus (Giebel); Handlirsch (1907) [7], p. 484, pl. 42, Figure 37.

Necrotaulius liasinus (Giebel); Handlirsch (1907) [7], p. 485, pl. 42, Figure 38.

Necrotaulius furcatus (Giebel); Tillyard (1933) [9], p. 62, Figures 23–25.

Necrotaulius stigmaticus Tillyard, 1933 [9], p. 65, Figure 27. *syn. nov.*

Necrotaulius westwoodi Tillyard, 1933 [9], pp. 64, 65, Figure 26. *syn. nov.*

Necrotaulius apicalis Tillyard, 1933 [9], p. 66, Figure 28. *syn. nov.*

Necrotaulius furcatus (Giebel); Willmann (1978) [51], p. 115.

Necrotaulius westwoodi Tillyard; Sukatsheva (1985) [52], p. 13, Figure 32.

Necrotaulius westwoodi Tillyard; Carpenter (1992) [29], p. 362, Figure 201,7.

Necrotaulius furcatus (Giebel); Jarzembowski (1999) [53], p. 159, text-Figures 18(A), 18(B).

Necrotaulius furcatus (Giebel); Jarzembowski and Palmer (2010) [54], p. 170, Figure 4.19.

Necrotaulius westwoodi Tillyard; Zhang et al. (2017) [18], p. 28, Figure 7(B).

Necrotaulius furcatus (Giebel); Zhang et al. (2017) [18], p. 28, Figure 7(C).

Holotype. YORYM YM 815/NHMUK I.11522 (Figure 4) from the Cotham Member of the Penarth Group (Rhaetian), Aust Cliff, Gloucestershire.

Remarks. The holotype of this species was originally reported as YM 815 [55] with the counterpart being sent to the "British Museum" (NHMUK) according to R. Wootton (note in specimen box at YORYM). NHMUK I.11522 was later reported as the holotype by Tillyard [9] who thought that the differences in the specimens were due to breakage after the original holotype figure. However, based on the original figure of the holotype by Brodie ([33], pl. 9, Figure 16) and writing on the rock of the specimens, it is clear that the first report was correct. YM 815 matches the holotype figure by Brodie ([33], pl. 9, Figure 16) and written on the rock in Brodie's handwriting is "Pl 9 F 16." Figure 4 shows the specimens involved and copies of the figures from [9, 33]. It

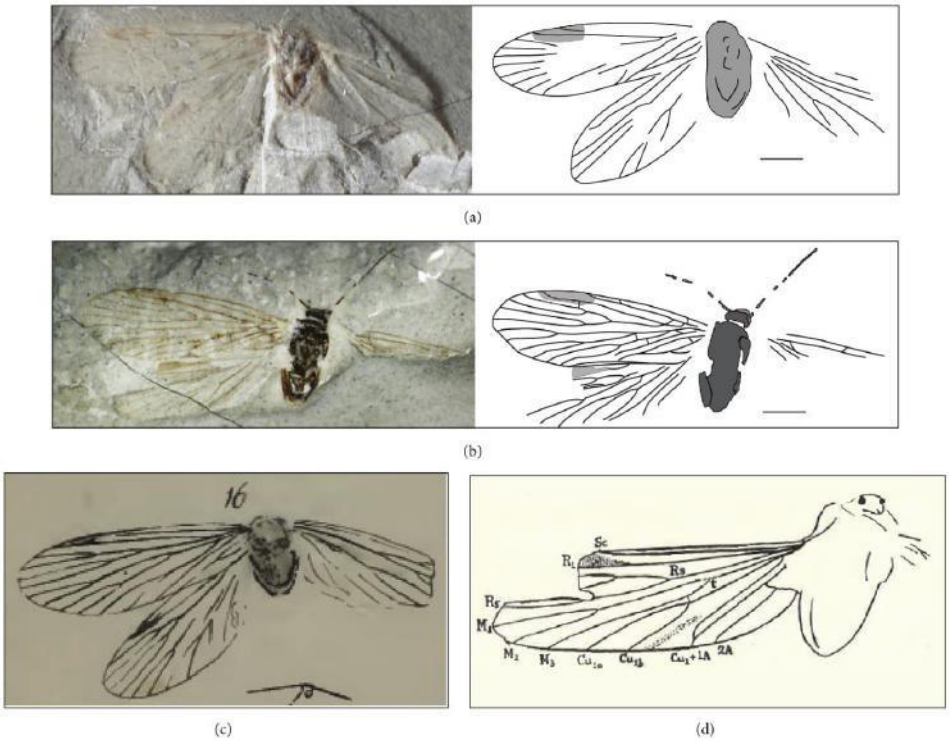

FIGURE 4: Holotype of *Austaulius furcatus* (Giebel, 1856) from Aust Cliff, Gloucestershire. (a) YORYM YM 815; (b) NHMUK I.11522; (c) original holotype figure in Brodie (1845, pl. 9, Figure 16); (d) figure of "holotype" in Tillyard (1933, Figure 25). Scale bars = 1 mm.

is unclear why Tillyard figured I.11522 without the very prominent left forewing (Figure 4(d)); he did suggest that the specimen had broken since Brodie's original figure, so perhaps it was further prepared after Tillyard had figured it, revealing the forewing. Although the part and counterpart look different, there is a calcite vein that cuts diagonally across the hindwing at the same position in both parts.

Additional Material. Rhaetian: NHMUK I.11545, I.11544 (previously holotype of *O. liasina*, figd Brodie [33, pl. 9, Figure 17]), I.11534; YORYM: YM1984/7F, YM1984/6F, YM1984/1F from Aust Cliff; I.3081 from Wainlode Cliff (previous holotype of *N. apicalis*, Figure 5(a)); one other in the private collection of RAC collected from Blue Anchor. Hettangian: I.11019 from Copt Heath; I.11584 from unknown locality in England ("W" on museum label) (previous holotype of *N. stigmaticus* Figure 5(b)); I.11761 (previous holotype of *N. westwoodi*, Figure 5(c)) and 11574 both from unknown localities in England.

Diagnosis. Forewings 4.3–5.6 mm in length, 1.4–1.8 mm in width. Anterior fork (F1) of Rs branching point is almost in line with the branching point of posterior fork (F2), or slightly distal.

Description. Holotype forewing 5.3 mm in length. It is an almost whole specimen with both forewings wholly preserved (one on each part); right hindwing nearly complete. Body, head, and antennae also preserved in the counterpart but poorly. One antenna with 15 antennomeres preserved including scape. In forewing Sc terminating on C just beyond mid-wing, with two cross-veins between Sc and C; R simple, reaching anterior margin in apical quarter of the wing within the pterostigma; oblique cross-vein near base between R and Sc; Rs splits from R in basal quarter further bifurcating into two forks of subequal length (posterior fork slightly longer than anterior). M lying very close to R at base and fused with CuA shortly after leaving CuP for a short distance; M bifurcates forming two forks, the anterior shorter than the posterior (this is clearest in the counterpart of the holotype, Figure 3); one cross-vein between M and CuA; CuP is preserved almost to the posterior margin; one cross-vein between CuA and CuP. Additional cross-vein between 1A and 2A near the base. Hindwings are poorly preserved but, in

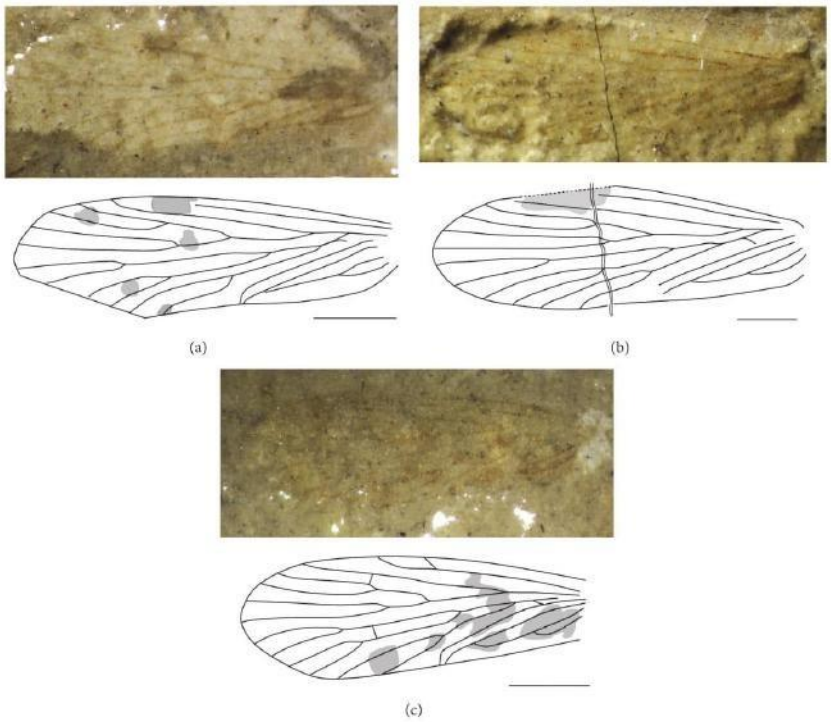

FIGURE 5: Previous holotypes now considered conspecific with *Austaulius furcatus* (Giebel, 1856). (a) *"Necrotaulius apicalis"* Tillyard, 1933 (NHMUK I.3081); (b) *"N. stigmaticus"* Tillyard, 1933 (NHMUK I.11584); (c) *"N. westwoodi"* Tillyard, 1933 (NHMUK I.11761), all from Wainlode Cliff, Gloucestershire. Scale bars = 1 mm.

the counterpart, it seems that the venation is similar except there are three veins in the medial system rather than four, the posterior vein being simple. Colour pattern evident in most specimens although it may be faint.

Remarks. The remaining species described by Tillyard [9] (*N. westwoodi*, *N. stigmaticus*, and *N. apicalis*) all show the fusion of M and Cu typical of *Austaulius*. The backward bent CuP is preserved in the holotype and in the previous holotypes of *N. apicalis* and *N. westwoodi*; in *N. stigmaticus* this character is not preserved but it can be assumed by its absence that it was desclerotised. Although the type specimens are less well preserved than the type of *A. furcatus*, and not all the cross-veins are visible, there is nothing significant to distinguish any of them as being different from *A. furcatus*, so they are considered to be junior synonyms. Tillyard drew the outlines of *N. stigmaticus* and *N. apicalis* with a more pointed tip than is apparent from the specimens. The holotypes of *N. westwoodi*, *N. stigmaticus*, and *N. apicalis* were collected from Wainlode Cliff and the holotype of *A. furcatus* was collected from Aust Cliff. Both localities were reported in Zhang et al. [18] as Early Jurassic (J_1) but the insect bearing horizon at these localities is found in the Penarth Group which is Late Triassic in age.

Austaulius haustrum sp. nov.

urn:lsid:zoobank.org:act:09920586-B224-437C-A567-46808E8D1AAE

Holotype. NHMUK II 3103 a and b (Figure 6), Sinemurian, Turneri Chronozone, Brooki Bed, Monmouth Beach, Lyme Regis, Dorset, UK. Collected by R. A. Coram.

Etymology. Haustrum is the original Latin word for "haustellum" indicating the presence of this character in the holotype.

Diagnosis. Forewing length 4.7 mm, width 1.8 mm. Anterior fork (F1) of Rs branches distally of branching point of posterior fork (F2), much further than in *A. furcatus*.

Description. The holotype is a well preserved specimen with two forewings and a partial hind wing, thorax, head, some antennomeres, some leg segments, maxillary and labial palps, and the haustellum. Pronotum is small and heavily sclerotized. Fore coxa broader than the fore femur, mid coxa appears broader but not well preserved. Head is hypognathous. Maxillary palps are longer than the labial palps, two

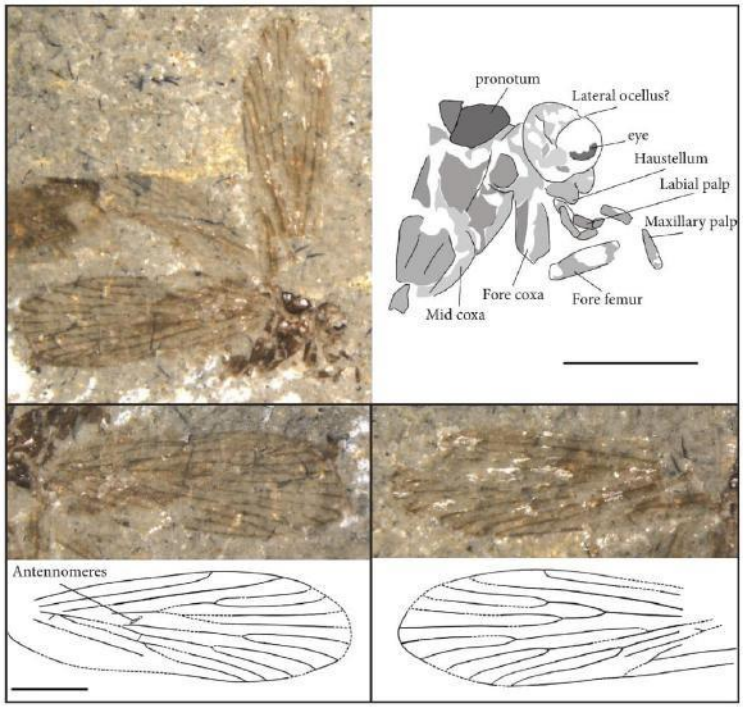

FIGURE 6: Holotype of *Austaulius haustrum* gen. et sp. nov. (NHMUK II 3103 a and b) from Monmouth Beach, Lyme Regis, Dorset. Bottom left figure is the right forewing of the holotype flipped so the costal margin is on top. Scale bars = 1 mm.

elongate segments of one palp preserved; three labial palp segments preserved (as well as another unidentified palp with two segments), attached to the haustellum. Eye socket appears large, but only a small portion of the actual eye is preserved and there is a groove above the eye where the lateral ocellus would be found. The apex of CuP appears to be desclerotised as in *A. furcatus*.

Remarks. This specimen was figured by Coram ([56], Figure 5) as a "Caddisfly-like necrotauliid." This is the only necrotauliid specimen to preserve the haustellum. As discussed in the introduction, this is the only specified adult synapomorphy for Trichoptera [22] and suggests that the Necrotauliidae are trichopterans.

5. Discussion

The necrotauliids have been considered to be primitive trichopterans, advanced stem-amphiesmenopterans, and a paraphyletic assemblage of primitive trichopterans, primitive lepidopterans, and stem-amphiesmenopterans. Therefore, necrotauliids represent an important group for understanding the evolution of the Amphiesmenoptera but much of the taxonomy of the group was in need of revision. Ansorge [12, 14] revised the Upper Lias German material, restricting the Necrotauliidae to two species and removing the family from Trichoptera, suggesting that *Liadotaulius* (Philopotamidae) was the only true trichopteran from the German Upper Lias.

English *Necrotaulius* are sparse and only three specimens were identified as *N. parvulus*; this is also the only species of this genus from the Lias of England. Most of the specimens previously attributed to *Necrotaulius* are herein considered to belong to a separate and older genus *(Austaulius)* which, based on the current fossil record, survived the end Triassic mass extinction but is not recorded after the appearance of *Necrotaulius* in England. This genus can be separated from *Necrotaulius* by the fusion of M and CuA near the base for a short distance.

The holotype of *A. haustrum* is well preserved and exhibits several mouthpart characters that are rare in amphiesmenopteran fossils. The head is visible with a partial eye preserved; ventral to the main head capsule there is a structure from which the labial palps originate. The labial palps appear to be formed of three elongated segments and would probably be about half the length of the maxillary palps as in extant Trichoptera [57]. The haustellum is the only

suggested autapomorphy for adult Trichoptera [25] and we propose that the structure in the holotype of *A. haustrum* ventral to the head and attached to the labial palps is the haustellum. It is a composite of the prelabium and the hypopharynx which forms a short proboscis used for sucking up liquids [22]; it is not homologous to the structure of the same name in Diptera [58]. For an in-depth description of the morphology of an adult trichopteran head see [58]; [25] provides a lateral photograph of a trichopteran head with a short haustellum and palps similar to those seen in the holotype of *A. haustrum*. The presence of a haustellum in the holotype of *A. haustrum* suggests that the family Necrotauliidae belongs to the Trichoptera.

Conflicts of Interest

None of the authors have conflicts of interest to declare.

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Appendix 6. UK occurrence data. CMF = Charmouth Mudstone Formation, WMF – Whitby Mudstone Formation, LF = Lilstock Formation, BLF = Blue Lias Formation, WF = Westbury Formation, Bcl.F = Beacon Limestone Formation; R = Rhaetian, H = Hettangian, S = Sinemurian, P = Pliensbachian, T = Toarcian; s&f = Saurian and Fish, I.Lim = Insect Limestone, land = Landscape Marble, flat = flatstones, wood = woodstones, top = topstones, interim = intermediate stones, yellow = yellowstones, n = nodules, t = tabular.

Order	Family	Genus	Full species	Locality	Fm	Stage		Substage		Zone	Bed
Blattodea	Caloblattinidae	Blat:Calo.gen.nov1	Blat:Calo.gen.nov1 sp.nov.1	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat
Blattodea	Caloblattinidae	Blat:Calo.gen.nov1	Blat:Calo.gen.nov1 sp.nov.1	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Blattodea	Caloblattinidae	Blat:Calo.gen.nov2	Blat:Calo.gen.nov2 sp.nov.2	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	NA
Blattodea	Caloblattinidae	Mesoblattopsis	Mesoblattopsis bensoni	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Blattodea	Caloblattinidae	Rhipidoblattina	Rhipidoblattina geikiei	Apperley	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Blattodea	Caloblattinidae	Rhipidoblattina	Rhipidoblattina geikiei	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA
Blattodea	Mesoblattinidae	Mesoblattina	Mesoblattina sp	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Blattodea	NA	Actinoblattula	Actinoblattula liasina	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Blattodea	Raphidiomimidae	Liadoblattina	Liadoblattina blakei	Alderton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Coleoptera	Buprestidae	Buprestites	Buprestites bractoides	Skelton	WMF	Toarcian	62	T1	66	Tenuicostatum	NA
Coleoptera	Chrysomelidae	Chrysomelopsis	Chrysomelopsis andraei	Forthampton	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera giebeli	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera schlotheimi	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera schlotheimi	Stratford	BLF	Hettangian	59	H1	59	Planorbis	NA
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera schlotheimi	Wilmcote	BLF	Hettangian	59	H1	59	Planorbis	NA
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera giebeli	Apperley	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera giebeli	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera pigmentatus	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera schlotheimi	Apperley	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera schlotheimi	Aust	LF	Rhaetian	58	R2	58	SAB2	land
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera schlotheimi	Brockeridge	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera schlotheimi	Forthampton	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera schlotheimi	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera schlotheimi	Tortworth	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera schlotheimi	Westbury	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera alisonae	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera alisonae	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi t
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera alisonae	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera giebeli	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera giebeli	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera schlotheimi	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera alisonae	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera alisonae	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera alisonae	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	yellow
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera alisonae	Catherston	CMF	Sinemurian	60	S2	63	Obtusum	top
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera alisonae	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	NA
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera giebeli	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera giebeli	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	interm
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera giebeli	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera giebeli	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	yellow
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera giebeli	Catherston	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera giebeli	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera giebeli	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	wood
Coleoptera	Coptoclavidae	Holcoptera	Holcoptera schlotheimi	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	NA
Coleoptera	Cupedidae	Liassocupes	Liassocupes parvus	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Coleoptera	Cupedidae	Liassocupes	Liassocupes maculatus	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Coleoptera	Cupedidae	Metacupes	Metacupes harrisi	Cnap Twt	BLF	Hettangian	59	H1	59	Planorbis	NA
Coleoptera	Cupedidae	NA	NA	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Coleoptera	Cupedidae	Stigmenamma	Stigmenamma heeri	Hasfield	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Dytiscidae	Dytiscidae	Dytiscidae sp	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Elateridae	Anepismus	Anepismus vanus	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Elateridae	Anepismus	Anepismus vanus	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Elateridae	Elaterina	Elaterina liassica	Lyme Regis	CMF	Sinemurian	60	S2	63	NA	NA
Coleoptera	Elateridae	Elaterophanes	Elaterophanes vetustus	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Coleoptera	Elateridae	Elaterophanes	Elaterophanes acutus	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Elateridae	Elaterophanes	Elaterophanes vetustus	Apperley	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Elateridae	Elaterophanes	Elaterophanes regius	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Elateridae	Elaterophanes	Elaterophanes regius	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Elateridae	Mimelater	Mimelater angulatus	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Elateridae	Mimemala	Mimemala giganteum	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Elateridae	Plastelater	Plastelater neptuni	Hasfield	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Elateridae	Stenelytron	Stenelytron redtenbacheri	Brockeridge	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Elateridae	Stenelytron	Stenelytron redtenbacheri	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Gyrinidae	Gyrinidae gen	Gyrinidae sp	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Coleoptera	NA	Ancylocheira	Ancylocheira liasina	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	NA	Anhydrophilus	Anhydrophilus brodiei	Craycombe	LF	Rhaetian	58	R2	58	SAB2	NA

Coleoptera	NA	Anhydrophilus	Anhydrophilus brodiei	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	NA	Bellingera	Bellingera ovalis	Aust	LF	Rhaetian	58	R2	58	SAB2	land
Coleoptera	NA	Coleopteron	Coleopteron aquaticus	Hasfield	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	NA	Hydrobiites	Hydrobiites anglicus	Hasfield	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	NA	Hydrobiites	Hydrobiites giebeli	Aust	LF	Rhaetian	58	R2	58	SAB2	land
Coleoptera	NA	Hydrobiites	Hydrobiites liasinus	Hasfield	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	NA	Paragyrinus	Paragyrinus dubius	Brockeridge	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	NA	Paragyrinus	Paragyrinus dubius	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	NA	Protocuneus	Protocuneus punctatus	Wilmcote	BLF	Hettangian	59	H1	59	Planorbis	NA
Coleoptera	NA	Pseudotelephorus	Pseudotelephorus haueri	Forthampton	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	NA	Pterostichites	Pterostichites grandis	Glen Parva	WF	Rhaetian	58	R1	57	SAB1	black shales
Coleoptera	NA	Xenogyrinus	Xenogyrinus natans	Forthampton	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Ommatidae	Liassocupes	Liassocupes maculatus	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Coleoptera	Ommatidae	Liassocupes	Liassocupes maculatus	Catherston	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Ommatidae	Liassocupes	Liassocupes maculatus	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Ommatidae	Liassocupes	Liassocupes parvus	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Ommatidae	Liassocupes	Liassocupes parvus	Catherston	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Ommatidae	Omma	Omma liassicum	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Coleoptera	Ommatidae	Omma	Omma liassicum	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA
Coleoptera	Ommatidae	Omma	Omma liassicum	Hasfield	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Coleoptera	Ommatidae	Omma	Omma liassicum	Norton	LF	Rhaetian	58	R2	58	SAB2	NA
Coleoptera	Ommatidae	Omma	Omma liassicum	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Permosynidae	Dinoharpalus	Dinoharpalus liasinus	Aust	LF	Rhaetian	58	R2	58	SAB2	land
Coleoptera	Schizophoridae	Tersus	Tersus crowsoni	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Coleoptera	Staphylinidae	Staphylinidae gen	Staphylinidae sp	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Dermaptera	Dermapteridae	Phanerogramma	Phanerogramma heeri	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Dermaptera	Dermapteridae	Phanerogramma	Phanerogramma heeri	Copt Heath	BLF	Hettangian	59	H1	59	Planorbis	NA
Dermaptera	Dermapteridae	Phanerogramma	Phanerogramma heeri	Apperley	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Dermaptera	Dermapteridae	Phanerogramma	Phanerogramma heeri	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA
Dermaptera	Dermapteridae	Phanerogramma	Phanerogramma heeri	Forthampton	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Dermaptera	Dermapteridae	Phanerogramma	Phanerogramma heeri	Norton	LF	Rhaetian	58	R2	58	SAB2	NA
Dermaptera	Dermapteridae	Phanerogramma	Phanerogramma heeri	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Dermaptera	NA	Trivenopteron	Trivenopteron moorei	Ilminster	BcLF	Toarcian	62	T1	66	Falciferum	s&f
Dermaptera	Protodiplatyidae	Brevicula	Brevicula gradus	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Dermaptera	Protodiplatyidae	Brevicula	Brevicula maculata	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Dermaptera	Protodiplatyidae	Brevicula	Brevicula gradus	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat
Dermaptera	Protodiplatyidae	Brevicula	Brevicula gradus	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	top
Dermaptera	Protodiplatyidae	Brevicula	Brevicula gradus	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Diptera	Anisopodidae	Megarhyphus	Megarhyphus amberae	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	brooki
Diptera	Chironomidae	Aenna	Aenna triassica	Aust	LF	Rhaetian	58	R2	58	SAB2	land
Diptera	Limoniidae	Architipula	Architipula anglicana	Alderton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Diptera	Limoniidae	Architipula	Architipula anglicana	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Diptera	Limoniidae	Grimmenia	Grimmenia tillyardi	Alderton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Diptera	Limoniidae	Mesotipula	Mesotipula slatteri	Alderton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Diptera	Limoniidae	Mesotipula	Mesotipula slatteri	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Diptera	Oligophrynidae	Oligophryne	Oligophryne britannica	Stonebarrow	CMF	Sinemurian	60	S2	63	Oxynotum	NA
Diptera	Ptychopteridae	Eoptychoptera	Eoptychoptera spectra	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Diptera	Rhaetaniidae	Rhaetania	Rhaetania dianae	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Diptera	Tanyderidae	Nannotanyderus	Nannotanyderus oliviae	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	brooki
Hemiptera	Archegocimicidae	Britannicola	Britannicola senilis	Apperley	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Hemiptera	Archijassidae	Archijassidae gen	Archijassidae sp	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Hemiptera	Belostomatidae	Belostomatidae gen	Belostomatidae sp	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Hemiptera	Belostomatidae	Lethonectes	Lethonectes naucoroides	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Hemiptera	Belostomatidae	Liassocorixa	Liassocorixa dorsetica	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Hemiptera	Belostomatidae	Liassocorixa	Liassocorixa dorsetica	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	wood
Hemiptera	Belostomatidae	Propreocoris	Propreocoris maculatus	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Hemiptera	Belostomatidae	Tarsabedus	Tarsabedus sp	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	nodules
Hemiptera	Belostomatidae	Tarsabedus	Tarsabedus menkei	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	NA
Hemiptera	Dysmorphoptilidae	Dysmorphoptila	Dysmorphoptila liasina	Apperley	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Hemiptera	Dysmorphoptilidae	Dysmorphoptila	Dysmorphoptila liasina	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA
Hemiptera	Dysmorphoptilidae	Dysmorphoptila	Dysmorphoptila liasina	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Hemiptera	Dysmorphoptilidae	Dysmorphoptila	Dysmorphoptila liasina	Westbury	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Hemiptera	Dysmorphoptilidae	Dysmorphoptila	Dysmorphoptila sp	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Hemiptera	Fulgoridiidae	Margaroptilon	Margaroptilon woodwardi	Ilminster	BnLF	Toarcian	62	T1	66	Falciferum	s&f
Hemiptera	Fulgoridiidae	Margaroptilon	Margaroptilon woodwardi	Alderton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Hemiptera	Fulgoridiidae	Margaroptilon	Margaroptilon woodwardi	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Hemiptera	Hylicellidae	Homopterites	Homopterites anglicus	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Hemiptera	NA	Mesocixiella	Mesocixiella fennahi	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Hemiptera	NA	Pachymerus	Pachymerus zucholdi	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Hemiptera	Pachymeridiidae	Neomeridium	Neomeridium trifurcum	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Hemiptera	Pachymeridiidae	Neomeridium	Neomeridium trifurcum	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Hemiptera	Procercopidae	Procercopis	Procercopis Hem:Proc.sp.nov.1	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA
Hemiptera	Procercopidae	Procercopis	Procercopis Hem:Proc.sp.nov.2	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA
Hemiptera	Progonocimicidae	Cicadocoris	Cicadocoris anglicus	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA

Hemiptera	Protocoridae	Protocoris	Protocoris indistinctus	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA	
Hemiptera	Pterocimicidae	Pterocimex	Pterocimex sp	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n	
Hemiptera	Pterocimicidae	Pterocimex	Pterocimex jacksoni	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood	
Hemiptera	Pterocimicidae	Pterocimex	Pterocimex jacksoni	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat	
Hemiptera	Tettigarctidae	Liassocicada	Liassocicada ignotus	Forthampton	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Hemiptera	Tettigarctidae	Liassocicada	Liassocicada ignotus	Hasfield	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Hemiptera	Tettigarctidae	Liassocicada	Liassocicada ignotus	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Hemiptera	Tettigarctidae	Shuraboprosbole	Shuraboprosbole rotruda	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n	
Hemiptera	Tettigarctidae	Shuraboprosbole	Shuraboprosbole rotruda	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat	
Hemiptera	Tettigarctidae	Shuraboprosbole	Shuraboprosbole rotruda	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	top	
Hemiptera	Tettigarctidae	Shuraboprosbole	Shuraboprosbole rotruda	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat	
Lepidoptera	Archaeolepiidae	Archaeolepis	Archaeolepis mane	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n	
Mecoptera	Bittacidae	Protobittacus	Protobittacus liassicus	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Bittacidae	Protobittacus	Protobittacus maculatus	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Bittacidae	Protobittacus gen	Protobittacus sp	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood	
Mecoptera	Eomeropidae	Jurachorista	Jurachorista bashkuevi	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	brooki	
Mecoptera	Liassophilidae	Liassophila	Liassophila hydromanicoides	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA	
Mecoptera	Mesochoristidae	Mesochorista	Mesochorista anglicana	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA	
Mecoptera	NA	Chauliodites	Chauliodites minor	Hotham	LF	Rhaetian	58	R2	58	SAB2	NA	
Mecoptera	Orthophlebiidae	Mesopanorpa	Mesopanorpa brodiei	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia liassica	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia liassica	Grafton	BLF	Hettangian	59	H1	59	Planorbis	NA	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia longissima	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia pictipennis	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia anglica	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia confusa	Forthampton	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia gracilis	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia intermedia	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia liassica	Apperley	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia liassica	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia liassica	Forthampton	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia liassica	Hasfield	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia liassica	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia liassica	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia liassica	Westbury	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia liassica	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	brooki	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia capillata	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia capillata	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood	
Mecoptera	Orthophlebiidae	Orthophlebia	Orthophlebia capillata	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat	
Mecoptera	Orthophlebiidae	Protorthophlebia	Protorthophlebia latipennis	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA	
Mecoptera	Orthophlebiidae	Protorthophlebia	Protorthophlebia latipennis	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA	
Mecoptera	Orthophlebiidae	Protorthophlebia	Protorthophlebia latipennis	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n	
Mecoptera	Orthophlebiidae	Protorthophlebia	Protorthophlebia latipennis	Charmouth	CMF	Sinemurian	60	S2	63	Obtusum	wood	
Mecoptera	Orthophlebiidae	Protorthophlebia	Protorthophlebia latipennis	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat	
Mecoptera	Pseudopolycentropidae	Pseudopolycentropus	Pseudopolycentropus triangularis	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood	
Mecoptera	Worcestobiidae	Worcestobia	Worcestobia gigantea	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Worcestobiidae	Worcestobia	Worcestobia gigantea	Westbury	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Mecoptera	Worcestobiidae	Worcestobia	Worcestobia nov.	Westbury	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Neuroptera	NA	Megapolystoechus	Megapolystoechus magnificus	Aust	LF	Rhaetian	58	R2	58	SAB2	land	
Neuroptera	NA	Megapolystoechus	Megapolystoechus magnificus	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Neuroptera	Prohemerobiidae	Actinophlebia	Actinophlebia sp	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n	
Neuroptera	Prohemerobiidae	Actinophlebia	Actinophlebia intermixta	Alderton	WMF	Toarcian	62	T1	66	Falciferum	s&f	
Neuroptera	Prohemerobiidae	Actinophlebia	Actinophlebia intermixta	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f	
Neuroptera	Prohemerobiidae	Actinophlebia	Actinophlebia Neur:Proh.sp.nov.1	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA	
Neuroptera	Prohemerobiidae	Prohemerobius	Prohemerobius Neur:Proh.sp.nov.2	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim	
Neuroptera	Prohemerobiidae	Prohemerobius	Prohemerobius Neur:Proh.sp.nov.3	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	brooki	
Neuroptera	Prohemerobiidae	Prohemerobius	Prohemerobius Neur:Proh.sp.nov.4	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	brooki	
Neuroptera	Prohemerobiidae	Prohemerobius	Prohemerobius aldertonensis	Alderton	WMF	Toarcian	62	T1	66	Falciferum	s&f	
Neuroptera	Prohemerobiidae	Prohemerobius	Prohemerobius complexus	Alderton	WMF	Toarcian	62	T1	66	Falciferum	s&f	
Neuroptera	Prohemerobiidae	Prohemerobius	Prohemerobius complexus	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f	
Odonata	Anglophlebiidae	Anglophlebia	Anglophlebia gigantea	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat	
Odonata	Archithemistidae	Archithemis'	Archithemis' brodiei	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f	
Odonata	Campterophlebiidae	Archithemis	Archithemis liassina	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA	
Odonata	Campterophlebiidae	Dorsettia	Dorsettia laeta	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat	
Odonata	Campterophlebiidae	Hypsothemis	Hypsothemis fraseri	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat	
Odonata	Campterophlebiidae	Lateophlebia	Lateophlebia anglicanopsis	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat	
Odonata	Campterophlebiidae	Petrophlebia	Petrophlebia anglicana	Barrow	BLF	Hettangian	59	H1	59	Planorbis	NA	
Odonata	Heterophlebiidae	Heterophlebia	Heterophlebia buckmani	Ilminster	BcLF	Toarcian	62	T1	66	Falciferum	s&f	
Odonata	Heterophlebiidae	Heterophlebia	Heterophlebia buckmani	Alderton	WMF	Toarcian	62	T1	66	Falciferum	s&f	
Odonata	Heterophlebiidae	Heterophlebia	Heterophlebia buckmani	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f	
Odonata	Liassogomphidae	Heterothemis	Heterothemis brodiei	Ilminster	BcLF	Toarcian	62	T1	66	Falciferum	s&f	
Odonata	Liassogomphidae	Heterothemis	Heterothemis brodiei	Alderton	WMF	Toarcian	62	T1	66	Falciferum	s&f	
Odonata	Liassogomphidae	Heterothemis	Heterothemis brodiei	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f	
Odonata	Liassophlebiidae	Liassophlebia	Liassophlebia magnifica	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA	

Odonata	Liassophlebiidae	Liassophlebia	Liassophlebia withersi	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Odonata	Liassophlebiidae	Liassophlebia	Liassophlebia sp	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	nodules
Odonata	Liassophlebiidae	Liassophlebia	Liassophlebia pseudomagnifica	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat
Odonata	Liassophlebiidae	Rossiphlebia	Rossiphlebia jacksoni	Catherston	CMF	Sinemurian	60	S2	63	Obtusum	flat
Odonata	Liassophlebiidae	Rossiphlebia	Rossiphlebia jacksoni	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Odonata	Protomyrmeleontidae	Protomyrmeleon	Protomyrmeleontidae sp	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Odonata	Triassolestidae	Progonophlebia	Progonophlebia woodwardi	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Bintoniellidae	Haglopsis	Haglopsis brodiei	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Bintoniellidae	Haglopsis	Haglopsis brodiei	Grafton	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Bintoniellidae	Haglopsis	Haglopsis parallela	Bickmarsh	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Bintoniellidae	Haglopsis	Haglopsis parallela	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Bintoniellidae	Haglopsis	Haglopsis parallela	Stratford	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Bintoniellidae	Haglopsis	Haglopsis brodiei	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Bintoniellidae	Haglopsis	Haglopsis parallela	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA
Orthoptera	Bintoniellidae	Haglopsis	Haglopsis parallela	Forthampton	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Bintoniellidae	Haglopsis	Haglopsis parallela	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Bintoniellidae	Haglopsis	Haglopsis parallela	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Bintoniellidae	Haglopsis	Haglopsis parallela	English Channel	BLF	Sinemurian	60	S1	62	Bucklandi	NA
Orthoptera	Elcanidae	Archelcana	Archelcana liasina	Bidford	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Elcanidae	Archelcana	Archelcana liasina	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Elcanidae	Archelcana	Archelcana liasina	Stratford	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Elcanidae	Archelcana	Archelcana liasina	Wilmcote	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Elcanidae	Archelcana	Archelcana liasina	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA
Orthoptera	Elcanidae	Archelcana	Archelcana liasina	Charfield	LF	Rhaetian	58	R2	58	SAB2	NA
Orthoptera	Elcanidae	Archelcana	Archelcana liasina	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Elcanidae	Archelcana	Archelcana liasina	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Elcanidae	Archelcana	Archelcana liasina	Westbury	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Elcanidae	Archelcana	Archelcana Orth:Elc.sp.nov.	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Elcanidae	Archelcana	Archelcana liasina	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat
Orthoptera	Elcanidae	Archelcana	Archelcana liasina	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Orthoptera	Elcanidae	Archelcana	Archelcana liasina	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Orthoptera	Elcanidae	Archelcana	Archelcana geinitzi	Alderton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Orthoptera	Elcanidae	Archelcana	Archelcana geinitzi	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Orthoptera	Elcanidae	Parelcana	Parelcana anglicana	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Haglidae	Hagla	Hagla gracilis	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Haglidae	Hagla	Hagla gracilis	Grafton	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Haglidae	Hagla	Hagla gracilis	Forthampton	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Haglidae	Hagla	Hagla gracilis	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Haglidae	Liassophyllum	Liassophyllum abbreviatum	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Haglidae	Orth:Hag.gen.nov.	Orth:Hag.gen.nov.sp.nov.	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Haglidae	Orth:Hag.gen.nov.	Orth:Hag.gen.nov.sp.nov.	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Haglidae	Protohagla	Protohagla langi	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Orthoptera	Locustopseidae	Locustopsis	Locustopsis lacoei	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Locustopseidae	Locustopsis	Locustopsis spectablis	Copt Heath	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Locustopseidae	Locustopsis	Locustopsis lacoei	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Locustopseidae	Locustopsis	Locustopsis spectablis	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Locustopseidae	Locustopsis	Locustopsis ornatum	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat
Orthoptera	Locustopseidae	Locustopsis	Locustopsis ornatum	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Orthoptera	Locustopseidae	Locustopsis	Locustopsis Orth:Loc.sp.nov.	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat
Orthoptera	Locustopseidae	Mesolocustopsis	Mesolocustopsis constricta	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Locustopseidae	Mesolocustopsis	Mesolocustopsis gracilis	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	NA	Liadolocusta	Liadolocusta auscultans	Forthampton	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Protogryllidae	Protogryllus	Protogryllus magnus	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Protogryllidae	Protogryllus	Protogryllus parallelus	Binton	BLF	Hettangian	59	H1	59	Planorbis	NA
Orthoptera	Protogryllidae	Protogryllus	Protogryllus grandis	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA
Orthoptera	Protogryllidae	Protogryllus	Protogryllus parallelus	Browns W	LF	Rhaetian	58	R2	58	SAB2	NA
Orthoptera	Protogryllidae	Protogryllus	Protogryllus grandis	Forthampton	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Protogryllidae	Protogryllus	Protogryllus grandis	Strensham	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Orthoptera	Protogryllidae	Protogryllus	Protogryllus magnus	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Orthoptera	Protogryllidae	Protogryllus	Protogryllus magnus	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Orthoptera	Protogryllidae	Protogryllus	Protogryllus magnus	Catherston	CMF	Sinemurian	60	S2	63	Obtusum	flat
Orthoptera	Protogryllidae	Protogryllus	Protogryllus acutipennis	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Orthoptera	Protogryllidae	Protogryllus	Protogryllus acutipennis	Gretton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Orthoptera	Protogryllidae	Protogryllus	Protogryllus magnus	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Orthoptera	Protogryllidae	Protogryllus	Protogryllus parallelus	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f
Orthoptera	Regiatidae	Micromacula	Micromacula gracilis	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Orthoptera	Regiatidae	Micromacula	Micromacula sp	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Orthoptera	Regiatidae	Micromacula	Micromacula gracilis	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Orthoptera	Regiatidae	Micromacula	Micromacula gracilis	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Orthoptera	Regiatidae	Regiata	Regiata scutra	Black Ven	CMF	Sinemurian	60	S1	62	Turneri	birchi n
Orthoptera	Regiatidae	Regiata	Regiata sp	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	brooki
Orthoptera	Regiatidae	Regiata	Regiata scutra	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	flat
Orthoptera	Regiatidae	Regiata	Regiata scutra	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Orthoptera	Regiatidae	Regiata	Regiata scutra	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Orthoptera	Regiatidae	Regiata	Regiata scutra	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	wood

Phasmatodea	Aerophasmatidae	Durnovaria	Durnovaria parallela	Stonebarrow	CMF	Sinemurian	60	S2	63	Obtusum	flat
Phasmatodea	Aerophasmatidae	NA	NA	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Raphidioptera	Mesoraphidiidae	Mesoraphidia	Mesoraphidia confusa	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	NA
Raphidioptera	Priscaenigmatidae	Priscaenigma	Priscaenigma obtusa	Black Ven	CMF	Sinemurian	60	S2	63	Obtusum	wood
Trichoptera	Necrotauliidae	Austaulius	Austaulius furcatus	Copt Heath	BLF	Hettangian	59	H1	59	Planorbis	NA
Trichoptera	Necrotauliidae	Austaulius	Austaulius furcatus	Aust	LF	Rhaetian	58	R2	58	SAB2	land
Trichoptera	Necrotauliidae	Austaulius	Austaulius furcatus	Blue Anchor	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Trichoptera	Necrotauliidae	Austaulius	Austaulius furcatus	Brockeridge	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Trichoptera	Necrotauliidae	Austaulius	Austaulius furcatus	Wainlode	LF	Rhaetian	58	R2	58	SAB2	I.Lim
Trichoptera	Necrotauliidae	Austaulius	Austaulius haustrum	Monmouth B	CMF	Sinemurian	60	S1	62	Turneri	brooki
Trichoptera	Necrotauliidae	Necrotaulius	Necrotaulius parvulus	Ilminster	BcLF	Toarcian	62	T1	66	Falciferum	s&f
Trichoptera	Necrotauliidae	Necrotaulius	Necrotaulius parvulus	Dumbleton	WMF	Toarcian	62	T1	66	Falciferum	s&f